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Annals of the Missouri Botanical Garden

SPECIES RECONSIDERED: CONSEQUENCES FOR BIODIVERSITY AND EVOLUTION. INTRODUCTION[1, 2]

P. Mick Richardson[3]

The Annual Systematics Symposium that took place at the Missouri Botanical Garden in 2003 marked a major milestone in the history of scientific discourse in the U.S.A. The Systematics Symposium is remarkable for its unbroken run of 50 years at the same institution. Also noteworthy is the fact that the National Science Foundation has supported 48 of the symposia. What is the explanation for such a long run of successful symposia, and why does each symposium continue to fill the seats of a large auditorium? Certainly, some of the audience comes for an annual visit to the massive herbarium or the comprehensive library, to visit a large city for shopping, or for the chance of an exotic meal, but most of the audience come to hear the symposium speakers. There is a distinct freshness to each symposium because every year the list of speakers is chosen by a new set of organizers. This year was no exception, and the organizers comprised a zoologist and a botanist. Jonathan Losos and Peter Stevens invited a diverse group of speakers to shed some light on the perennial subject of "the species question."

In order to bring attention to a display of Linnaean material in the Monsanto Research Building, the new location of the library, a Special Linnaean Celebration Talk was arranged on the Friday evening, an atypical time for one of our symposium talks. This was delivered by Mary P. ("Polly") Winsor. Although it is published here with the succinct title "Linnaeus's biology was not essentialist," it was advertised and delivered with the intriguing title "Would you like your species concept rare, sir, or well-done? (A look at how the history of science is cooked, how you can tell, and whether it is any good for you anyway)." The room was filled to overflowing, and especially notable in the audience were the local history of science professionals, a group not always seen at the symposium.

Saturday, as usual, was the main day of the symposium. Jonathan Losos moderated the morning session, and Peter Stevens was the afternoon moderator. Peter Raven introduced the evening speakers, a husband and wife team of scientists. All but one of the speakers has submitted a manuscript in time for publication here.

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[1] This and the seven articles that follow it are the proceedings of the 50th Annual Systematics Symposium of the Missouri Botanical Garden, *Species Reconsidered: Consequences for Biodiversity and Evolution.* The symposium was held 10–11 October, 2003, at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

The symposium was supported in part by the National Science Foundation under grant DEB-9981642. I thank Jonathon Losos and Peter Stevens for selecting an interesting diversity of speakers. I also thank Sandy Lopez and Mary McNamara for their dedicated organizational and administrative assistance, Mary Merello and Amy Pool for their help with the registration process, and Alina Freire-Fierro for her expertise in producing the symposium booklet and getting the information onto the Garden website in a timely fashion. Last but not least, I wish to thank the speakers for making the symposium so wonderfully interesting.

[2] The editors of the *Annals* thank Sophia Balcomb for her editorial contribution to these papers.

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LINNAEUS'S BIOLOGY WAS NOT ESSENTIALIST[1]

Mary P. Winsor[2]

Abstract

The current picture of the history of taxonomy incorporates A. J. Cain's claim that Linnaeus strove to apply the logical method of definition taught by medieval followers of Aristotle. Cain's argument does not stand up to critical examination. Contrary to some published statements, there is no evidence that Linnaeus ever studied logic. His use of the words "genus" and "species" ruined the meaning they had in logic, and "essential" meant to him merely "taxonomically useful." The essentialism story, a narrative that has most pre-Darwinian biologists steeped in the world view of Plato and Aristotle, is ill-founded and improbable.

Key words: A. J. Cain, essentialism, history of systematics, history of taxonomy, Linnaeus, E. Mayr.

The Missouri Botanical Garden has celebrated the 250th anniversary of the publication of Linnaeus's *Species Plantarum* (Linnaeus, 1753), but there are doubtless some biologists who are not sure if they are proud of that landmark. After all, we have now departed so far from the beliefs of that eccentric old Swede that it is rather embarrassing to count him among our intellectual ancestors. Didn't he think that every species was directly created by God, in other words, wasn't he a creationist and thus an enemy of evolution? More profoundly, didn't Linnaeus believe that every species has its own essence, that is, type in the Platonic sense? Well, to be blunt, no, and no. His views on the fixity of species changed in his lifetime, and the business about essentialism is the scholarly equivalent of an urban myth, that is, a story everyone repeats but for which there is scant basis in fact.

That the mature Linnaeus abandoned his youthful insistence on the fixity of species was pointed out by Edward Greene (1909) and fully documented by John Ramsbottom (1938). Linnaeus was perfectly comfortable imagining that God may have made, in His original burst of creativity, only one species per genus, while natural processes later caused the emergence of the others. Although it is very well known that Linnaeus underwent this shift from absolute fixity to limited transmutation (Larson, 1971; Koerner, 1999; Müller-Wille, 1999), I remind you of it because it so clearly contradicts the urban myth about essentialism. The whole point about Platonic types, we have been told time and again, is that there are unbridgeable gaps separating them. Did the mature Linnaeus think that some species were created with an immutable essence and others with mutable essences? Ernst Mayr deserves credit for admitting the problem (1982: 259), but he leaves us to conclude that Linnaeus was hopelessly confused and inconsistent. I suggest that it is we who are confused, for we attribute to Linnaeus a philosophical notion he never held.

Actually, I suspect that many of us are allowing the spectre of modern creationism to bias our understanding of a pre-Darwinian creationist like Linnaeus. To a modern biologist who does not believe in God, Linnaeus's explicit piety has the effect of making the essentialism story seem plausible, but the link connecting these realms was the insight of a later generation. In 1857 Louis Agassiz, disturbed by the rising interest in evolution, argued in his "Essay on Classification" that the Creator had conceived each species in his divine intellect before giving it material existence (Winsor, 1991). He repeated these ideas after Darwin's revolutionary book appeared in 1859, and Agassiz remained adamant that the patterns recorded by taxonomists were direct evidence of God's thoughts. But all this was a century after Linnaeus. In Linnaeus's day the "requirements of Christian faith," contrary to Mayr's claim (1982: 259), did not forbid the possibility that the "kinds" mentioned in the Book of Genesis could have been at the taxonomists' rank of genus rather than species. Those modern biologists who do believe in God will have more sympathy with Linnaeus than with Agassiz, because they accept that the Creator willed into existence our actual world,

[1] My research was supported by a grant from the Social Sciences and Humanities Research Council of Canada, for which I am very grateful. For their assistance and encouragement I also thank Stephan Müller-Wille and my students Abby Slinger, Jennifer Hertz, Elise Paradis, and Dennis Yeung. I am particularly indebted to Peter Stevens and Peter Raven for inviting me to the Missouri Botanical Garden's 50th Annual Systematics Symposium, and I thank Mick Richardson for arranging such a pleasant visit.

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including life with all its evolutionary complexity and history. Those biologists realize that belief in God does not logically entail belief in the fixity of species.

The mature Linnaeus's limited transmutation was, Mayr (1982: 259) admits, "not only inconsistent with everything he had said and believed before but was in fact irreconcilable with essentialism." It is time, then, to look more carefully at this supposed doctrine or dogma of essentialism. Without a doubt, there does exist today a story about essentialist beliefs in past centuries. It is this story, that is, this historical claim about the world-view of past taxonomists, that I am challenging. (Some philosophers are now refurbishing the word essentialism for variously modernized concepts of natural kinds, but the biological and historical literature to which I refer was innocent of such sophistication. Whether concepts of natural kinds corresponding to such 21st century usage were held in the past is an entirely separate question not relevant here [Boyd, 1999: 152; Ellis, 2002].) I begin by laying before you only one telling of the essentialism story, but it stands for other repetitions that number in the thousands, if we include undergraduate lectures. The latest edition of one of the most widely used textbooks, *Evolutionary Biology* by Futuyma (1998: 448), puts it this way:

> Linnaeus and other early taxonomists held what Ernst Mayr (1942, 1963)[3] has called a "TYPOLOGICAL" or "ESSENTIALIST" NOTION OF SPECIES. Individuals were members of a given species if they sufficiently conformed to that "type," or ideal, in certain characters that were "essential" fixed properties—a concept descended from Plato's "ideas" (see chapter 1).

Here are the relevant passages in his chapter 1 (Futuyma 1998: 6):

> In positing an evolutionary process wherein natural selection sorts among hereditary variations, *Darwin identified variation as a centrally important fact of biological systems*. In doing so, he broke with a 2000-year-old tradition that had dominated Western thought. The tradition stemmed from Plato, whose philosophy was built on the concept of the "eidos," the "form" or "idea," a transcendent ideal form imperfectly imitated by its earthly representations. In his famous metaphor of the cave in *The Republic*, Plato likened earthly objects, such as the triangles or horses we are familiar with, to the shadows cast on the wall of a cave by objects that pass by the entrance. Like people within the cave, bound so that they face the wall, we see only the shadows, the imperfect representations, of reality. Likewise, the reality—the ESSENCE—of the true equilateral triangle is only imperfectly captured by the triangles we draw or construct, all of which are imperfect, and vary from the true, essential triangle. And so it is with horses, or any other species: each has an eternal, immutable essence, but each individual has imperfections. In this philosophy of ESSENTIALISM, variation is accidental imperfection; only essences matter.
>
> Plato's philosophy of essentialism became incorporated into Western philosophy. Its central tenet was that however much the objects in a class might accidentally vary, the class still had a defining essence that could not change. Thus each species—horse, zebra, or ass, for instance—has an essence, and one cannot be changed into another any more than a triangle can vary enough to become a rectangle.

The chief source of this historical narrative is Ernst Mayr (1959, 1963, 1968, 1976, 1982), whose words have carried such authority that his claims have been rarely questioned. Yet in its broad sweep across the history of systematics, this story is not merely inaccurate in particulars, it is wrong and harmful in its basic message. According to the essentialism story, Platonic idealism dominated Western thought until Darwin broke its spell, whereas in fact, William of Ockham in the 14th century and other nominalists dealt it crushing blows from which it never recovered. Systematic biology evolved, largely independent of philosophy, from the 16th century onward, through the actions of an army of herbalists, encyclopedists, makers and cataloguers of collections, and other naturalists, whose joint efforts built up the mountain of data that Linnaeus confronted. None of Linnaeus's numerous enemies noticed any remnant of Plato's ideal forms in the series of catalogues the Swedish professor and his followers kept churning out. Quite the contrary, one philosopher later noted with surprise and respect that naturalists' success in their massive project of inventory seemed to involve an active neglect of the classic rules of logical definition (Whewell, 1847; Winsor, 2003). By suppressing this rich history, the essentialism story distorts the historical and logical foundation of Darwinism.

To fully understand the creation and impact of the essentialism story would require us to take it apart and examine it piece by piece, but at present I will limit my attention to the claim that Linnaeus himself was in thrall to this philosophy. Mayr's sources for this claim are impressive, including such scholars as James Larson (1971) and Frans Stafleu (1971). Yet a close examination of all Mayr's sources reveals that instead of a literature of accumulating evidence, all derive from a single source, an article by Arthur J. Cain in the *Proceedings of the Linnean Society of London* (1958). There the Oxford zoologist maintained that Linnaeus thought in terms of Aristotelian essences; the backbone of his claim is that "the method [Linnaeus] adopted was to classify by the rules of Logical Division, which involve the determination

[3] Mayr does set out the essentialism story on pp. 4–6 and 16–17 of his 1963 book (using only the term "typological"), but not in his 1942 book.

of the essence of each entity" (Cain, 1958: 162). Cain's conclusions are now woven into the fabric of established knowledge, repeated countless times by people who have never read him. Scholars who subsequently contributed fresh research on Linnaeus, ironically including Cain himself (Broberg, 1985; Stevens & Cullen, 1990; Cain, 1992, 1993, 1994, 1995; Müller-Wille, 1999) are perceived, if they are read at all, as supplementing Cain's 1958 conclusions, even though they paint a very different picture.

A few years ago I undertook a careful examination of Cain's 1958 article as part of a project concerned with why some scientists turn their attention to questions about the past (Winsor, 2001). My intention was to investigate the phenomenon of scientists turning to history, and both Cain and Mayr were in the prime of their scientific careers when they began to write about history in the 1950s. My interest was Cain's motivation, not Linnaeus's reputation, but I found myself amazed by the many weaknesses in Cain's argument. It would seem that Cain's conclusions took hold because they meshed so well with two other semi-independent and simultaneous lines of thought. One was Mayr's association of the morphological concept of species with typology, which included tracing typology back to Plato's cave (Mayr et al., 1953: 15; Mayr, 1976: 256–257). Another strand flowed from David Hull's 1965 article "The effect of essentialism on taxonomy—two thousand years of stasis." The essentialism story known today consists of elements from each strand, which were twisted tightly together in 1968 when Mayr decided that the concept of species he called "typological thinking" could be equated with the concept of essentialism he found in Hull. I intend to trace out elsewhere the distinct history of those three strands.

Cain believed he had made a breakthrough in understanding Linnaeus when he learned that Aristotelian logic mandated that definition should proceed by stating the kind (*genus* in Latin) to which a species belongs (man is an animal) and then stating the *differentia*, the features that distinguish it from the other members of that kind (man is a rational animal). Linnaeus's rule that every species name must begin with the name of the genus to which it belongs was what had first made Cain suspicious, and then the telltale words *definitio, differentia*, and *essentialis* seemed to confirm it. Indeed the case seemed beyond doubt when Cain found a series of incriminating pronouncements in Linnaeus's *Philosophia Botanica*, which he rendered as "The *Essential Character* of a genus is that which gives some characteristic peculiar to it, if there is one such, which will instantly serve to distinguish it from all others in the same natural order [*Phil. Bot.*, 187] .... The true specific name is a *Differentia essentialis* (*Phil. Bot.*, 257) distinguishing that species from all others in the same genus.... The *Character essentialis* [of a species] is a Differentia (*Phil. Bot.*, 258)" (Cain 1958: 148). These words of Linnaeus equipped Cain to argue that however messy and complicated his system became in practice, fundamentally Linnaeus must have been engaged in this sterile scholastic game.

The game was indeed scholastic, for the procedure of formulating definitions *per genus et differentiam* was an exercise familiar to generations of scholars in medieval universities, based upon the 6th century scholar Boethius's commentaries on and Latin translation of the 3rd century Greek scholar Porphyry's introduction to Aristotle (Kretzmann et al., 1982; Spade, 1994). Porphyry's notorious "five words" are rendered by Boethius *genus, species, differentia, propria*, and *accidens*. What Cain did not realize was the extent to which teachers in Linnaeus's day, and indeed many of the medieval schoolmen, regarded the whole business as a taxonomy of words, not things (Arnauld & Nicole, 1662). (What Aristotle himself would have thought of it [Balme, 1980, 1987: 73; Gotthelf, 1985] is quite another matter.) If the task is to define the word "horse," a schoolboy learned not to mention the features peculiar to his own mare Rosalind, such as her location and color, and not to compose a tedious list of all those features, such as being four-legged and having a mane and tail, that she shares with asses and zebras; the frugal and proper approach is simply to state the group name ("equine") plus the features distinguishing horses from others of this group. It was widely understood that this elementary exercise arouses the thorny question of whether the abstract "horse" (the universal), the idea or type of horsiness to which Rosalind somehow belongs, really enjoys existence in some eternal place, as Plato said, or has a more limited existence as the active power within each individual horse, as Aristotle said, or exists only nominally, as a product of our own mind, as William of Ockham said. Philosophers debated the question, but the relevant point here is that their debate did not touch the rules of proper definition. Even for a nominalist, it is efficient to describe an object that resembles other objects by first stating the set of similar things, and then pointing to the features by which this one differs.

The supposedly essentialist views Cain quoted from Linnaeus could have been multiplied, for Linnaeus also declared "The concept of a species consists of an essential feature, by which alone it is distinguished from all others in the same genus.... A specific definition contains features in which the species differs from those in the same genus. But the specific name contains the essential features of the defini-

tion. . . . Therefore the specific name is the essential definition" (Linnaeus, 1751: 219–220). (Note that for Linnaeus, the "name" of the species was not its two-word shorthand form, but the genus name modified by up to a dozen adjectives.) However, it would be a sin against a prime principle of historiography (understanding actions and words in the context of their own time) if we were to assume that Linnaeus was using the word *essentialis* in the same sense as medieval philosophers had. The context, as well as his own definition, shows that the word only meant "taxonomically useful" and nothing more. What he called the "character" of a genus was the list or suite of features found to be dependable, and these he categorized with three adjectives: *factitius*, *essentialis*, and *naturales*. The first was a single feature used in some botanist's artificial system; the second was a single feature, or as few as possible, peculiar enough that it serves to distinguish this genus from the other genera in its natural order. The third was the full list of features. The *character essentialis* was desirable because it enabled the production of a succinct catalog. Nowhere did Linnaeus suggest that the "essential" features were any closer to the inner nature of a plant than its other features. On the contrary, he insisted that botanists pursue the *characteres naturales*. Linnaeus (1751: 143) wrote,

> If the essential characters of all genera had been discovered, the recognition of plants would turn out to be very easy, and many would undervalue the natural characters, to their own loss. But they must understand that, without regard for the natural character, no one will turn out to be a sound botanist; for when new genera are discovered, the botanist will always be in doubt if [he] neglects the natural character. Anyone who thinks that he understands botany from the essential character and disregards the natural one is therefore deceiving and deceived; for the essential character cannot fail to be deceptive in quite a number of cases. The natural character is the foundation of the genera of plants, and no one has ever made a proper judgement about a genus without its help; and so it is and always will be the absolute foundation of the understanding of plants.

In erecting these terms, Linnaeus may have had in mind the famous exchange between John Ray and Joseph Pitton de Tournefort (Sloan, 1972; McMahon, 2003), but if so, he was siding with Ray and thumbing his nose at Tournefort, by choosing to define *essentialis* solely by its taxonomic convenience rather than by reference to a plant's essential nature.

The telltale words that had first caught Cain's attention, "genus" and "species," actually testify most damagingly against his claim that Linnaeus was following the rules of logical division. As every medieval schoolboy knew, Boethius's *genus* and *species* were relative terms. One may correctly say that "bird" is a *genus* containing the *species* "swan," but it is equally true that "bird" is a *species* in the *genus* "animal." A person devoted to scholastic principles, who decided to set up a system running from Kingdoms containing Classes to Classes containing Orders, would be obliged to avoid the logical terms *genus* and *species* for the next two ranks, for each Class is a *species* with respect to its Kingdom, but a *genus* with respect to its Orders. The fact that Linnaeus appropriated these old words and spoiled them by attaching them to absolute ranks in his hierarchy proves his utter disregard for the "Aristotelian" rules of logic.

I am myself no expert on Linnaeus, so I was relieved to find that the skepticism to which I was led by a close reading of Cain had already been independently adopted by Staffan Müller-Wille (1999) through his close reading of Linnaeus. His work, which is not yet as well known as it deserves to be, makes me confident that the tide of opinion on this issue must turn. Yet the process will not be easy, for the essentialism story can bias our reading without our noticing. Consider one significant detail from Mayr's *Growth of Biological Thought* (1982: 173): "In school Linnaeus had excelled in logic, and he was evidently deeply impressed by the precision of this method." Here we have an instance of history by deduction, for Cain's argument certainly does require us to imagine that Linnaeus had mastered scholastic logic. Yet Cain had no evidence to that effect, so he could only beguile his readers by saying that "every well-educated man in and before Linnaeus's time might have been given some instruction in the principles of classification in general, as laid down by Aristotle. This he would receive in the study of *Logic*. . . " (Cain, 1958: 145). Notice the ambiguity of the pronoun "he," which could easily be misread as "Linnaeus" though it properly refers only to some "well-educated man." Leaving aside the quibble that Linnaeus was not particularly well-educated by 18th century standards, Cain's claim is true only because of his carefully qualified verb "might have been given." An educated man might have studied Aristotelian logic, but then again, he might not.

Actually there is no evidence that Linnaeus studied logic at all, much less excelled at it, according to Müller-Wille (pers. comm.). Indeed the positive assertion of excellence in school is peculiarly at odds with the slight evidence we do have. Among Mayr's sources, the one that reports on Linnaeus's schooling, Blunt (1971: 18), says this:

> In 1724 he passed, though with no great distinction, into the Gymnasium. Here the curriculum was designed to fit the needs of boys intended for the priesthood; the emphasis was upon Greek, Hebrew, theology, meta-

physics and oratory—subjects in which he was little gifted and even less interested. Apparently he shone at physics and mathematics. . . .

This is an accurate summary of Linnaeus's own autobiography, which claims excellence in science and makes no mention of logic (Fries, 1923). The erroneous tidbit about his not only studying logic but being deeply impressed by it may now be hard to erase, however, because of being stated so clearly in Mayr's authoritative book.

The essentialism story that engulfed and incorporated Cain's 1958 argument also transformed it. Absent from Cain's article is the very word "essentialism," which had been used by Karl Popper (1944: 94) to expose a fallacious and dangerous habit of thought. The fallacy is one into which reasonable people are prone to fall, namely, to believe that we can find out the true nature of something by concocting a definition of the word that names it. (Actually Popper assumed that no 20th century scientist really believed this, so he aimed his criticism at "methodological essentialism," which means acting as though one believes it.) Popper's 1945 book *The Open Society and Its Enemies* further developed the concept, but there is no evidence that either Cain or Mayr took notice. David Hull's 1965 paper, which featured Popper's word and concept, was almost certainly how Mayr learned of them; Hull mailed him a copy of his paper, which was the start of Mayr's mentorship of Hull. (Mayr very graciously allowed me to examine their correspondence along with his other papers in the Harvard University Archives.) Hull recognized that there were some problems with Cain's argument (Hull, 1965: 316n, 1967, 1985), but he did not quarrel with Cain's basic message, that Linnaeus was in the business of defining species like a logician rather than describing them like a natural historian. The connection between Popper's concept and what bothered Mayr—"typological thinking" about species—was somewhat loose (Mayr considered Plato rather than Aristotle the enemy), but in general, Cain's assessment of Linnaeus seemed to fit into both Hull's and Mayr's views of the history of taxonomy.

When we consider how deeply Linnaeus was steeped in the literature and traditions of early modern botany and zoology, is it even likely that he would have fallen into the fallacy of essentialism? We need to realize that Popper was by no means the first thinker to warn people against it. The rhetoric of the Scientific Revolution, including the writings of Bacon, Descartes, and Locke, was consistently anti-scholastic. It was clear to every student of Linnaeus that the business of the true botanist was to interrogate nature; after all, he had emphasized that his own classes and orders were artificial devices, invented to ease identification.

What about Mayr's concern that individual differences, so crucial for Darwinian evolution, would have been discounted as mere accidents by any follower of classic logic? Cain later showed (1996) that the logicians' concept of "accident" had considerably faded by John Ray's time, but Mayr was surely correct that taxonomists wanted to find constant characters and did their best to weed out variable characters. This was obviously a practical issue, but whether the concepts of scholastic logic played any role at all in 18th century taxonomy, or even in the two previous centuries, entirely remains to be demonstrated.

Unfortunately, the essentialism story has tended to dampen interest in the rich and complex story of exactly how taxonomists, both before and after Darwin, coped with the real-world challenges of comparing and identifying organisms. To loosen its grip, we could begin by recognizing that maligning Linnaeus distorts our understanding of the entire history of systematics.

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PROBLEMS WITH SPECIES: PATTERNS AND PROCESSES OF SPECIES FORMATION IN SALAMANDERS[1]

David B. Wake[2, 3]

ABSTRACT

How many species one recognizes within a given taxon remains a difficult question, especially when morphology is relatively stable or when clinal variation is present, thus complicating diagnosis. I accept the general lineage concept of species, and my goal is to recognize historically distinct evolutionary lineages that are likely to remain distinct. Here I analyze this task with respect to patterns of species formation in two genera of plethodontid salamanders in California. *Ensatina* is a ring species complex surrounding the Central Valley of California. At present it is a single species with seven subspecies that are linked by apparent clinal variation in intergrade zones, but there are also some narrow hybrid zones where morphologically and ecologically differentiated forms interact. In contrast, *Batrachoseps*, which has much the same distribution, has about 20 species in California, most occurring in sympatry with *Ensatina*. Divergence in the two taxa is based on two fundamentally different phenomena, and yet there are some common themes. Adaptive divergence in coloration is the dominant theme in *Ensatina*, whereas differentiation is largely perceived at the molecular level in *Batrachoseps*. Yet both have evolved in the same region and have been affected by many of the same climatic and earth historical phenomena. Within the *Ensatina* complex, different adaptations related to predator avoidance have evolved. Coloration has diverged in different directions in coastal and inland populations, even though genetic interactions continue to take place. Where coastal populations meet other coastal populations, ecologically and morphologically similar populations merge genetically, even if well differentiated in molecular traits. In contrast, where the ring is crossed and where ecologically and morphologically differentiated populations meet, they hybridize narrowly or are sympatric and behave as if they are species. Within the ring-like distribution, clinal patterns of variation occur. The current polytypic taxonomy is retained, even though it is problematic, because alternatives are even less appropriate. In contrast, where genetically differentiated populations of *Batrachoseps* meet they typically do not merge. Instead, they replace one another spatially, in part because they are so similar ecologically. Apparently the periods of isolation were sufficiently long that even in the absence of adaptive divergence there has been divergence of isolating mechanisms. Analysis of patterns of genetic differentiation in allozymes and mtDNA in relation to the geological history of California is used to generate biogeographic scenarios to help explain the contrast between *Batrachoseps* and *Ensatina*.

Key words: *Batrachoseps*, California paleogeography, *Ensatina*, historical biogeography, phylogeography, salamanders, species formation.

Every generation of biologists is destined to deal with species problems, sometimes repeatedly, or, in my case, continuously throughout my career. I described my first new species in 1962, based on a single specimen from Colombia that had been collected in the nineteenth century and assigned to a species that was thought, mistakenly, to range throughout Middle America and into South America (Brame & Wake, 1962). That species has so far stood the test of time, although even today it is known from fewer than 10 specimens. The decision to describe the species was based solely on anatomy and color pattern. The vast majority of all known species of salamanders is based on such criteria. When molecular methods became accessible to systematists, roughly 35 years ago, many surprises resulted. Kay Yanev, the first to use such methods in my lab, found that allozymes uncovered different patterns than did morphology in the Slender Salamanders (*Batrachoseps* Bonaparte, 1839) of California (Yanev, 1978). Several nominal species were species complexes, and a number of undescribed species were identified (Yanev, 1978). James Hanken, also in my lab, made similar observations on tropical salamanders of the genus *Thorius* Cope, 1869 (Hanken, 1980). Richard Highton was among the first systematists to use molecular

[1] Many individuals have collaborated with me in the research summarized here, and I thank especially C. Brown, M. Frelow, R. Hansen, E. Jockusch, S. Kuchta, C. Moritz, T. Papenfuss, D. Parks, C. Schneider, N. Staub, M. Wake, T. Wake, and K. Yanev. C. Brown permitted me to use many of his excellent photographs of *Ensatina*. The figures are by Karen Klitz. I appreciate the helpful comments of Shawn Kuchta and two anonymous reviewers. Financial support for my research from NSF, the Gompertz Professorship of my university, and the Museum of Vertebrate Zoology is gratefully acknowledged.

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[3] I dedicate this paper to R. C. Stebbins, who remains an enthusiast for *Ensatina*, on the occasion of his 91st birthday, and to the memory of Arden H. Brame Jr. II (1934–2004), who first introduced me to *Batrachoseps* and its diversity.

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methods in comprehensive geographic sampling; soon he uncovered levels of differentiation that were previously unimaginable (e.g., Highton, 1989). Before the main impact of the new molecular systematics revolution, the first modern complete catalog of amphibians reported 356 salamander species (Frost, 1985). The number of salamanders has increased since by 56% (the most recent count is 556, AmphibiaWeb, 2006). These are surprising increases for a group of relatively well-known terrestrial vertebrates, especially given that many of the new species reflect new discoveries. However, the new descriptions also highlight a modern species problem that is not unique to salamanders, but common to most taxa—how to translate molecular findings into taxonomy.

At the same time as new laboratory methodologies were drawing attention to species problems, new phylogenetic methods were having a major impact. In particular, methods ranging from mainly phenetic numerical taxonomy to cladistics were causing systematists to rethink species concepts and criteria (e.g., Cracraft, 1989, 1997; Mayden, 1997). As genetic analyses became ever more sophisticated, renewed focus on species was one result (e.g., Templeton, 1989; Coyne & Orr, 2004; Hey, 2001).

Given the sheer volume of recent publication on species concepts and on the species problem in general, it is a bit surprising that de Queiroz (1998, 2000, 2005) concluded that no fundamental change in our species concept has taken place and that such a change is unnecessary. I agree with this perspective. There are indeed many ongoing debates about species, but these are fundamentally about criteria and the debate is mainly joined by proponents of different kinds of data or more explicit methodologies than used in the past.

Here I examine patterns of species formation in Californian salamanders that display contrasting patterns. My goal is to highlight the connection of pattern and process in the formation of species. I am especially interested in comparisons of tree-based and character-based methods of delimiting species and what it is that we have delimited using these methods. In addition, I explore whether species recognition and delimitation is an exercise in recovering history or in predicting the likely course of further evolution.

I accept the general lineage concept of species that has been developed by Mayden (1997) and de Queiroz (1998, 2005). Species are historical lineages of metapopulations, or, more precisely, they are segments of metapopulation lineages; all other considerations are secondary to this primary principle. In any given instance, one might rely on any of a number of secondary species concepts as criteria to delineate what species are recognized. The critically important point with respect to the general concept is that there are no *necessary* attributes of species; rather, there are different lines of evidence that can be used concerning separation of lineages and these are all contingent. The pragmatic matter of delimiting species remains, however, and many methods have been proposed to deal with the issue. All are problematic (reviewed by Sites & Marshall, 2004). Furthermore, even adopting the concept framed by de Queiroz does not mean that different taxonomists will reach the same conclusions because criteria can be interpreted in different ways. I suspect that de Queiroz (based on de Queiroz, 2005) would recognize more species than I would in most instances, because of his emphasis on detection of initial splits.

Pattern and Process in Species Formation

Classifications of modes of species formation may be pattern-based or process-based. By pattern I refer in particular to geographic units inferred to be independently evolving lineage segments, i.e., species. Criteria vary greatly, from some relative measure of degree of divergence to tree-based approaches. The simplest way to explain such patterns is vicariance plus something else, such as differential selection or even haphazard changes in gene frequencies. By process I refer specifically to adaptive processes that are critically important to the establishment of independent lineages. Although an enormous amount of literature deals with species formation, I focus here on adaptive divergence and nonadaptive radiation. These are alternative ways that lineages diversify. The main problem that has been identified with adaptive divergence is the establishment of genetic isolation between the adaptively diverging populations when they are not allopatric. The main problem with nonadaptive radiation is the historic one of determining the status of geographically isolated but phylogenetically related parts of lineages, the classical problem with allopatry.

Adaptive Divergence

Papers by Bush (e.g., Bush, 1969) and a book by Endler (1977) are the starting points for my own interest in adaptive divergence (as opposed to the historical allopatry arguments) as a factor in species formation. Bush emphasized adaptive divergence in sympatry. Endler was more interested in geographic variation, in particular clines in characters or gene frequencies, and appearance of steps in clines, which might be preludes to species formation; his emphasis was parapatry or alloparapatry.

My studies of adaptive divergence have focused on the plethodontid salamander *Ensatina* Gray, 1850, which displays geographical differentiation interpreted as clinal differentiation and adaptive divergence on the way to species formation (Stebbins, 1949); it remains problematic whether subsets of the lineage have achieved independence and how many species warrant recognition. *Ensatina* is a ring species complex, a taxonomically challenging group of populations spread from British Columbia to Baja California, generally west of the Cascade-Sierra Nevada mountain system. These are terrestrial salamanders that never enter water, and they never gather in assemblages. They display direct development (lecitotrophy) in which embryos form inside the egg capsules and hatch as miniatures of the adult. *Ensatina* is relatively long-lived (ca. 8 years), sedentary, philopatric, and shows little dispersal (Stebbins, 1954; Staub et al., 1995). Prior to Stebbins (1949) four species were recognized, and although some originally had been described as members of the genus *Plethodon*, *Ensatina* long has been recognized as monophyletic (e.g., Dunn, 1926). Three of the species, *Ensatina croceater* (Cope, 1868), *E. klauberi* Dunn, 1929, and *E. platensis* (Jiménez de la Espada, 1875), were boldly marked (spotted or blotched) salamanders associated with forested regions from inner montane areas from Mount Lassen, California, southward to San Diego County and northern Baja California. A more widespread species, *E. eschscholtzii* Gray, 1850, was more uniformly colored, lacking spots or blotches, and was distributed along the coast of California and inland as well, to the Cascade Mountains in Oregon, Washington, and British Columbia. This form is associated with woodlands in the north, but in central and southern California it frequently occurs in more open habitats such as coastal sage scrub and chaparral.

The conclusions of Stebbins's (1949) groundbreaking study were revolutionary. He postulated that the four, then-recognized, species were part of a single lineage that had originated in the north and had expanded its range southward, adaptively diverging in different directions in the coastal and inland mountains. Stebbins recognized seven subspecies (*Ensatina eschscholtzii eschscholtzii*, *E. e. croceater*, *E. e. klauberi*, *E. e. oregonensis* (Girard, 1856), *E. e. picta* Wood, 1940, *E. e. platensis*, *E. e. xanthoptica* Stebbins, 1949; Fig. 1). He envisioned an ancestor having the traits of *picta*, restricted now to the ancient forests of southwestern Oregon and extreme northwestern California. This form has a somewhat variegated color pattern, and in it Stebbins envisioned the potential of all of the patterns found elsewhere. Each subspecies was diagnosed on the basis of its color pattern and some subtle morphological differences, although *oregonensis* was something of a default and had highly variable color patterns. From a *picta*-like ancestor Stebbins postulated southward migrations accompanied by divergent adaptation. In the Sierra Nevada the forms became restricted to montane areas, usually with closed canopy forests, and these were thought to show progressive stages in the development of disruptive coloration, from intergrades in the far north to spotted red and brown *platensis*, to more vivid yellow and black *croceater* in the Tehachapi Mountains, finally culminating in the boldly blotched *klauberi* in the far south (Fig. 1). Along the coast the generalized *oregonensis* is variable within and among populations in coloration, displaying generally cryptic coloration, but not disruptive in pattern. As populations became increasingly associated with more open habitats, a mimicry relationship developed with the dangerously poisonous newts (*Taricha* Gray, 1850). Mimicry is most highly developed in *xanthoptica*, mainly found in the inner coast ranges east of San Francisco Bay (Kuchta, 2005). These aposematically colored animals display vivid yellow and orange coloration that contrasts sharply with the disruptive patterns of the blotched inland forms. Adaptive divergence was accelerated as a result of these alternative adaptations, each different from the ancestral condition. When the contrasting *eschscholtzii* and *klauberi* contact each other at the southern extent of their ranges, they look and act like different species (Fig. 1), although they often hybridize. Critical to Stebbins's interpretation was a "transvalley leak," a relatively recent invasion of the coastal *xanthoptica* into the foothills of the Sierra Nevada, where it came into contact with *platensis* and the two hybridized. The ring was formed by the intergrading populations of *picta*, *oregonensis*, and *platensis* at the northern end of the Sacramento Valley.

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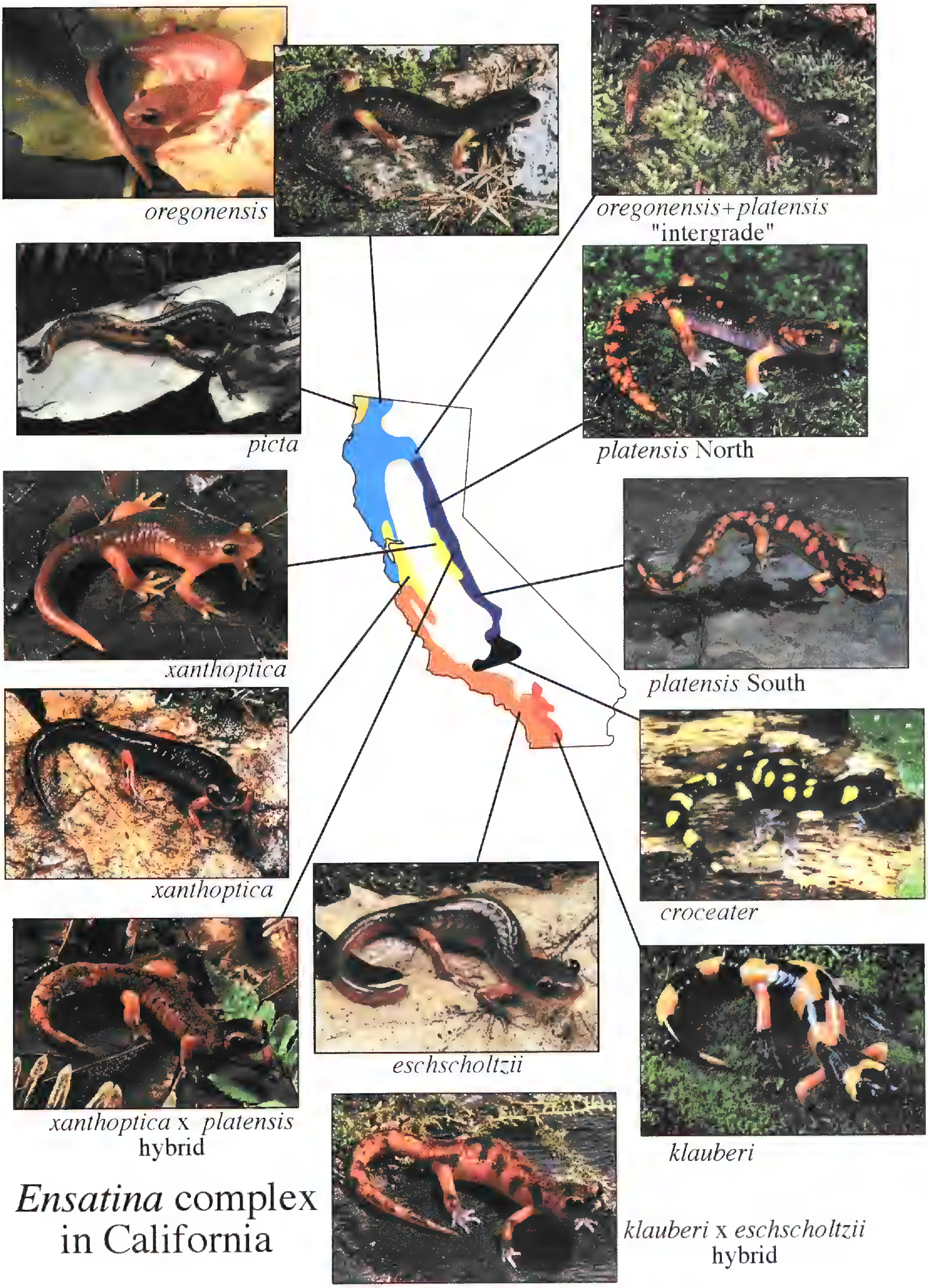
Figure 1. *Ensatina* that are found in California (all except the first mentioned photographed in that state). Diverse color patterns of the subspecies of *Ensatina*. Clockwise from upper left: *Ensatina eschscholtzii oregonensis* from Kittitas Co., Washington (photo by D. B. Wake); *E. e. oregonensis* from Sonoma Co. (C. W. Brown); intergrade between *E. e. oregonensis* and *E. e. platensis* from Shasta Co. (C. W. Brown); northern *E. e. platensis* from Calaveras Co. (C. W. Brown); southern *E. e. platensis* from Tulare Co. (D. B. Wake); *E. e. croceater* from Kern Co. (C. W. Brown); *E. e. klauberi* from San Diego Co. (C. W. Brown); *E. e. eschscholtzii* from San Diego Co. (C. W. Brown); at bottom, a presumptive F_1 hybrid between *E. e. klauberi* and *E. e. eschscholtzii* from San Diego Co. (C. W. Brown); a hybrid backcross between *E. e. xanthoptica* and *E. e. platensis* from Calaveras Co. (C. W. Brown); *E. e. xanthoptica* from Sonoma Co. (C. W. Brown); *E. e. xanthoptica* from Calaveras Co. (C. W. Brown); *E. e. picta* from Del Norte Co. (C. W. Brown).


oregonensis
oregonensis+platensis
"intergrade"
picta
platensis North
xanthoptica
platensis South
xanthoptica
croceater
eschscholtzii
xanthoptica x platensis
hybrid
klauberi
klauberi x eschscholtzii
hybrid
Ensatina complex
in California

Subsequent research lent some support to the hypothesis of Stebbins, but added complexity. Although some hybridization occurs in southern California, there is much more in the Sierra Nevada (Brown, 1974). At the southern-most point of contact in San Diego County, no current or past hybridization has been detected (Wake et al., 1986). Many evolutionists picked up on this example as one illustrating stages in a gradual process of species formation driven by adaptive divergence. *Ensatina* became a textbook example. Dobzhansky (1958) extended the hypothesis by envisioning gene flow throughout the ring retarding species formation and leading to the persistence of hybridization in the center of the ring and in the south. Stebbins (1949) had not discussed gene flow; he was thinking not of a continuous process but one in which there was fragmentation, isolation, and divergence, and then recontact. In other words, his view had elements of both vicariance and adaptive divergence. It was his biogeographical scenario that led him to consider it a ring species (Stebbins, pers. comm.).

When genetic methods became available I initiated studies of *Ensatina*, expecting it to be a complex of several to many species. Indeed, we found extensive genetic differentiation in allozymes (Wake & Yanev, 1986), but thought our sampling density too coarse to detect species borders (for a contrary view, see Highton, 1998). Differentiation was greater at the south end of the distribution than in the region across the upper end of Sacramento Valley, and *xanthoptica* and *platensis* were less differentiated from each other than were *eschscholtzii* and *klauberi*, as would be predicted by the Stebbins model. Many of the genetic distances between adjacent samples were relatively high, and we suspected that finer sampling was necessary to find either species borders or the gradual genetic transitions as expected under an isolation by distance scenario. We could readily reject Dobzhansky's hypothesis of ongoing gene flow throughout the complex. In general, the coastal forms clustered with the widespread *oregonensis*, and the blotched and spotted forms in the south clustered together in phenetic analyses of the allozyme data. However, the blotched *platensis* was highly differentiated, with northern populations clustering with the unblotched coastal forms and the single southern population analyzed clustering with *croceater* and *klauberi*.

In order to provide further resolution we expanded research to many populations extending from *picta* in northwestern California to *klauberi* in the south (Jackman & Wake, 1994). The populations resolved into three general clusters, within which patterns of isolation by distance were detected (Jackman & Wake, 1994). A northern cluster included what Stebbins (1949) had labeled *picta*, *picta/oregonensis* intergrades, *oregonensis*, and *oregonensis/platensis* intergrades. A second cluster included only *platensis* from the northern and central Sierra Nevada, and the final cluster included *platensis* from the southern Sierra Nevada as well as *croceater* and *klauberi*. Northern *platensis* was closer to populations in the northern cluster than to southern *platensis*, but a population from Wagner Ridge, west of Yosemite National Park, was intermediate between the two groups.

We investigated these patterns in more detail using the mitochondrial cytochrome b gene (Moritz et al., 1992). As expected, by examining distributions of haplotype clades, sharp borders between groups of populations were found, notably between northern and southern *platensis*. We also found a sharp break between northern *platensis* and *oregonensis/platensis* intergrades. The scale still seemed too coarse, and subsequently we expanded the sampling to saturate the California range of the genus, including nearly 400 samples (Kuchta et al., in prep.). Based on several different analyses we found it convenient to recognize 11 clusters of haplotypes (Fig. 2) based on patterns of phylogenetic relationships and geographic distribution. Most of these are well supported statistically, but some (e.g., B) appear to be paraphyletic and others (e.g., E) include members of two currently recognized subspecies. The northern (postulated ancestral forms) *picta* and *oregonensis* comprise six of these groups. Again, northern and southern *platensis* are differentiated, with southern populations clustering tightly with *croceater* (Fig. 2); there are three clades in this cluster, each with strong support.

More detailed study of the Sierra Nevada contact zone focused on the hybrid zone between *platensis* and *xanthoptica* (Wake et al., 1989). This transition is sharp, involving 8 fixed or nearly fixed allozymic markers that change in only a few hundred meters. The hybrid zones have been stable for about 40 years (first recorded by Brown, 1974), and may have narrowed over a 20-year period (Alexandrino et al., 2005). The distinction between the brightly colored, lowland *xanthoptica* and the cryptic, upland *platensis* occurs in an ecotone between lower elevation open oak-pine forest and chaparral and higher elevation closed canopy mixed conifer forest. Few F_1 hybrids are found, but there are many backcrosses. Because parental types are syntopic, they would be considered distinct species by most taxonomists were it not for the pattern in the remainder of the complex. The distribution of *xanthoptica* extends for about 100 km in the foothills of the Sierra Nevada. These populations are little differentiated from coastal populations of *xanthoptica* in allozymes and mtDNA, as well as coloration. Hybridization has only been studied in

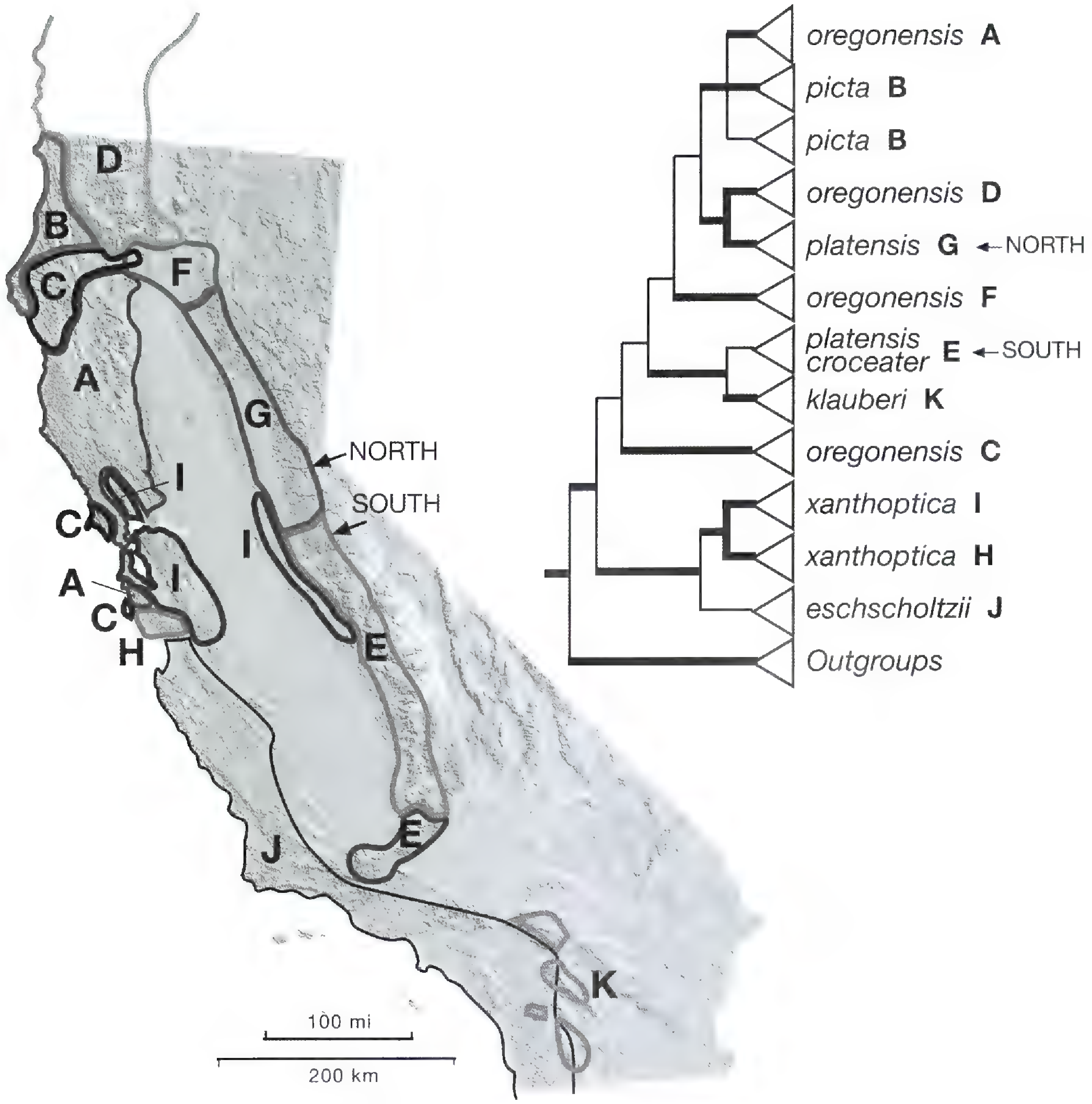


Figure 2. *Ensatina* in California. Left. Distribution of haplotype clades identified using the mitochondrial DNA gene cytochrome b. Right. Phylogram of Bayesian analysis of cytochrome sequences for nearly 400 samples of *Ensatina* from throughout the range of the genus. This is a preliminary analysis from a study in progress (Kuchta et al., in prep.). Clades with posterior probability of support at levels from 95%–100% are shown with thick lines. Some of the groups are not clearly clades, but they consist of relatively closely allied haplotypes that are geographically contiguous. The terminal groups are labeled and keyed to the map.

detail in the north (Alexandrino et al., 2005), but hybrid zones are also known to occur between southern *platensis* and *xanthoptica*. In contrast, where northern and southern *platensis* interact there is no evident difference in coloration or habitat preference. The genetic distance (Nei, 1972) between "pure" northern and southern *platensis* is 0.26–0.30, with major frequency differences in three loci. The genetic transition as determined from allozymes takes place over about 300 km, but a major transition in haplotypes takes place near the southern end of this region, about 75 km south of the major zone of allozymic transition (Wake & Schneider, 1998). Extraordinary variation in color pattern is found in Yosemite Valley. This is where the allozyme transition first is detected, and I believe that the variation may be a consequence of the merger of two genetically differentiated populations.

Jackman and Wake (1994) presented a possible scenario to account for the historical biogeography of *Ensatina* in the Sierra Nevada. They envisioned an early southward migration and differentiation of spotted and blotched salamanders, then geographic isolation as a result of a gap in the distribution that developed midway along the Sierra Nevada. Subsequently the northern Sierra Nevada was occupied by precursors of northern *platensis*, which in turn became isolated from *oregonensis* by repeated volcanism and glaciation in the region of present-day Mt. Lassen, in

northeastern California. Northern and southern *platensis* remained separated, probably by glaciation concentrated in the deep valleys of the central Sierra Nevada associated with the present-day Tuolomne, Merced, and San Joaquin river canyons, until late Pleistocene, when the two groups met and merged genetically. A selective sweep is responsible for rapid northward movement of the strongly adaptive blotched color pattern of southern *platensis* (Wake & Schneider, 1998). This pattern is postulated to have spread to the northern end of the range of the northern *platensis* haplotype group, in the Mt. Lassen area. Stebbins (1949) thought that populations in northeastern California were intergrades between *oregonensis* and northern *platensis*. An alternative interpretation is that strongly marked (but not blotched) salamanders in this area that differ from northern *platensis* in both allozymes and mtDNA might be an indication that southern *platensis* color alleles have only recently reached this area (e.g., Fig. 1), where they are introgressing into *oregonensis*.

The combination of allozymic and haplotype information led Highton (1998) to conclude that there is a broad hybrid zone separating northern and southern *platensis*, which he considered to be separate (but unnamed) species. He was silent with respect to coloration. However, in my view, the zone of interaction is far too broad (at least 75 km) to be considered a hybrid zone. I consider a hybrid zone to be a site either where two different parental forms co-occur and form hybrid individuals, or where two different parental forms are separated by a distance equivalent to a few, on the order of tens, of home ranges, with the intervening area occupied by hybrids and perhaps several generational backcrosses. I have argued elsewhere (Wake, 1997) that any of several suggestions for taxonomic change are problematic, and have retained the taxonomy of Stebbins (1949) until compelling evidence of species borders around (as contrasted with across) the ring-like distribution of *Ensatina* is found. When morphologically and ecologically similar forms meet they merge genetically, across haplotype clade borders, which remain as markers of past distributional limits. In contrast, when morphologically and ecologically differentiated forms meet they hybridize, in ecotones in which both parental forms are present. No indication of post-mating isolation is found. The hybrids and backcrosses are hypothesized to be at an adaptive disadvantage to either parental class, and we have measured extraordinary levels of selection against them (ca. 46%–75%) (Alexandrino et al., 2005). The classic explanation by Stebbins (1949) that intergradation occurs in the north, hybridization in the region of the transvalley leak in the middle, and sympatry in the south is correct, but the intergradation in the north may be secondary rather than primary, and sympatry with no hybridization is found in only one of four hybrid zones in the south. While sympatry with no hybridization is found at one site in the extreme south, hybridization is documented for three other *klauberi* isolates (Wake et al., 1986).

The situation on the coast is far from simple. There are two separate haplotype groups associated with distinctive allozymic-based clusters of populations within *xanthoptica*, one on the southern San Francisco Peninsula and the other widely distributed to the north and east of San Francisco Bay, including in the Sierran foothills. There are complex interactions where *oregonensis* (with two haplotype groups in the region) meets *xanthoptica* north and south of San Francisco Bay (Fig. 2; Wake, 1997). Furthermore, *eschscholtzii* is more differentiated (with respect to haplotypes) than would have been anticipated from the early allozyme study, with distinctive northern and southern geographic segments that form only a weakly supported possible clade.

These considerations led me to propose an historical biogeographic hypothesis for the complex, approximately 5 million years before present, which postulates a widely distributed *oregonensis/platensis* precursor in the north, an isolated precursor of northern *platensis* in the northern Sierran region, and a precursor of southern *platensis/croceater/klauberi* in the southern Sierran region (Wake, 1997). The Central Valley of California was at this time an inland extension of the Pacific Ocean, and the precursors of *xanthoptica/eschscholtzii* may have originated on an archipelago (cf. *Batrachoseps* scenario, below). How they got to the archipelago is uncertain, but because the land associated with the Salinian Block originated in the south, Parks (2000) postulated that an early movement of *oregonensis*-like salamanders southward gave rise both to northern *platensis* and to the precursors of *xanthoptica/eschscholtzii*. Subsequent orogenic as well as plate movements led to the assembly of populations of *Ensatina* into the current form of a ring. Whereas *klauberi* has usually been envisioned as well-nested within the complex, this alternative view (shown in Fig. 2, although the branching near the base of the complex is not well supported) is that *xanthoptica* + *eschscholtzii*, which form a distinctive phylogeographic unit, might form a clade that is sister to everything else, even including the diverse populational groups identified as *oregonensis* or *picta*. Some of Stebbins's subspecies are historical units that can be diagnosed by morphology and molecular characters (*klauberi*, *xanthoptica*, *eschscholtzii*); others are either nonmonophyletic amalgams (*platensis*) or incompletely differentiated

but adaptively diverged groups (southern *platensis-croceater*, *picta-oregonensis*). Finally, *oregonensis* is an undiagnosable grouping of differentiated lineages that branched independently (Fig. 2).

Ensatina illustrates a complicated relationship between adaptive divergence (as exemplified by the evolution of aposematic coloration in association with mimicry in the coastal populations, and cryptic coloration in the inner montane populations) and vicariant events (for example, the differentiation of northern and southern *platensis*). While our understanding of the complex has changed greatly since the work of Stebbins (1949), the basic point that this is a case in which adaptive divergence has been dominant still holds. This understanding does not help us to establish a better taxonomy, and with the present data, no alternative seems more appropriate than maintaining what we now have, a polytypic species. Establishing taxonomic species within the complex creates new problems. For example, *platensis* is readily diagnosable on morphological grounds, but not with either DNA (diphyletic) or proteins, and *croceater*, also diagnosable on morphological grounds is nested within southern *platensis* in the DNA tree. I conclude that this is a rare instance in which subspecies are helpful. They reflect what is in essence the shallowest (most recent) time depth, related to current adaptive antipredator strategies. At an intermediate time level are the genetic interchanges associated with population-level mergers around the ring, revealed by allozymes. Finally, the deepest level is reflected in the exclusive distributions of the haplotype groups recognized in Figure 2, all of which have discrete geographic limits and may reflect, in part, allopatric episodes at different times in the past.

Nonadaptive Radiation

The Slender Salamanders, genus *Batrachoseps*, have a geographic range in California that is similar to that of *Ensatina* (Fig. 3), but in other respects they are a sharp contrast to *Ensatina*. Species of *Batrachoseps* occur in syntopy with *Ensatina* at most sites of range overlap, including a vast array of habitats ranging from temperate rain forest in northwestern California, to relatively high elevations (ca. 2000 m) in the forests of the Sierra Nevada, to chaparral and coastal sage scrub along the southern coast. Like *Ensatina*, these are strictly terrestrial salamanders that lay direct-developing eggs on land. They are sedentary, with home ranges that are even smaller than those of *Ensatina*; there is little evidence of dispersal.

A detailed morphological analysis of *Batrachoseps* (Hendrickson, 1954) recorded extensive geographic variation and concluded that only a single species, *B. attenuatus* (Eschscholtz, 1833), was represented in California. A related northern species, *B. wrightorum* (Bishop, 1937), was found in the northern Cascade Mountains of Oregon. Hendrickson's conclusions were controversial because his two subspecies of *B. attenuatus* occurred in complete sympatry on Santa Cruz Island, off the coast of southern California. This unusual taxonomy resulted from his envisioning a complex biogeographic scenario in which the island was invaded by two somewhat differentiated populations, one from the north and the other from the south, establishing sympatry that formed from a ring-like pattern of differentiation (he was strongly influenced by the work of his adviser, R. C. Stebbins, on *Ensatina*).

Subsequent research revealed many species borders, and currently 20 species of *Batrachoseps* are recognized. Only one, *B. wrightorum*, is not found in California. Analysis of allozymic and mtDNA data sets identifies six major clades, all found in California. Species belonging to different clades often are so similar morphologically that they cannot be discriminated without molecular analysis. The three members of the subgenus *Plethopsis* Bishop, 1937, the sister taxon of subgenus *Batrachoseps*, differ from the latter in some osteological traits, and while most species of subgenus *Batrachoseps* are more slender than those of *Plethopsis*, one (*B. stebbinsi* Brame & Murray, 1968) closely resembles species of *Plethopsis*. At the molecular level, however, *B. stebbinsi* is sharply diverged from *Plethopsis*, differing both in allozymes (more than 10 fixed differences in conservatively evolving proteins) and in mtDNA sequences (Wake et al., 2002).

Along the coast of California clades replace one another geographically (Figs. 3, 4). The *attenuatus* clade in the north is replaced by the *pacificus* clade in the central coastal region, and it in turn is replaced by the *nigriventris* clade to the south, which finally is replaced by another member of the *pacificus* clade in the far south. Ecological transitions between the borders of the group are almost imperceptible, and the species represented are similar in morphology, including coloration, and ecology. In the central coastal region, the *pacificus* clade is represented by four morphologically similar species that once again replace one another from north to south. Furthermore, in southern California a geographical replacement pattern is found within the *pacificus* clade, starting with one species on the northern Channel Islands and a second on the southern Channel Islands and adjacent mainland. The most southerly member of the *pacificus* clade, *B. major* Camp, 1915, has several clearly distinguished haplotype clades within it, and

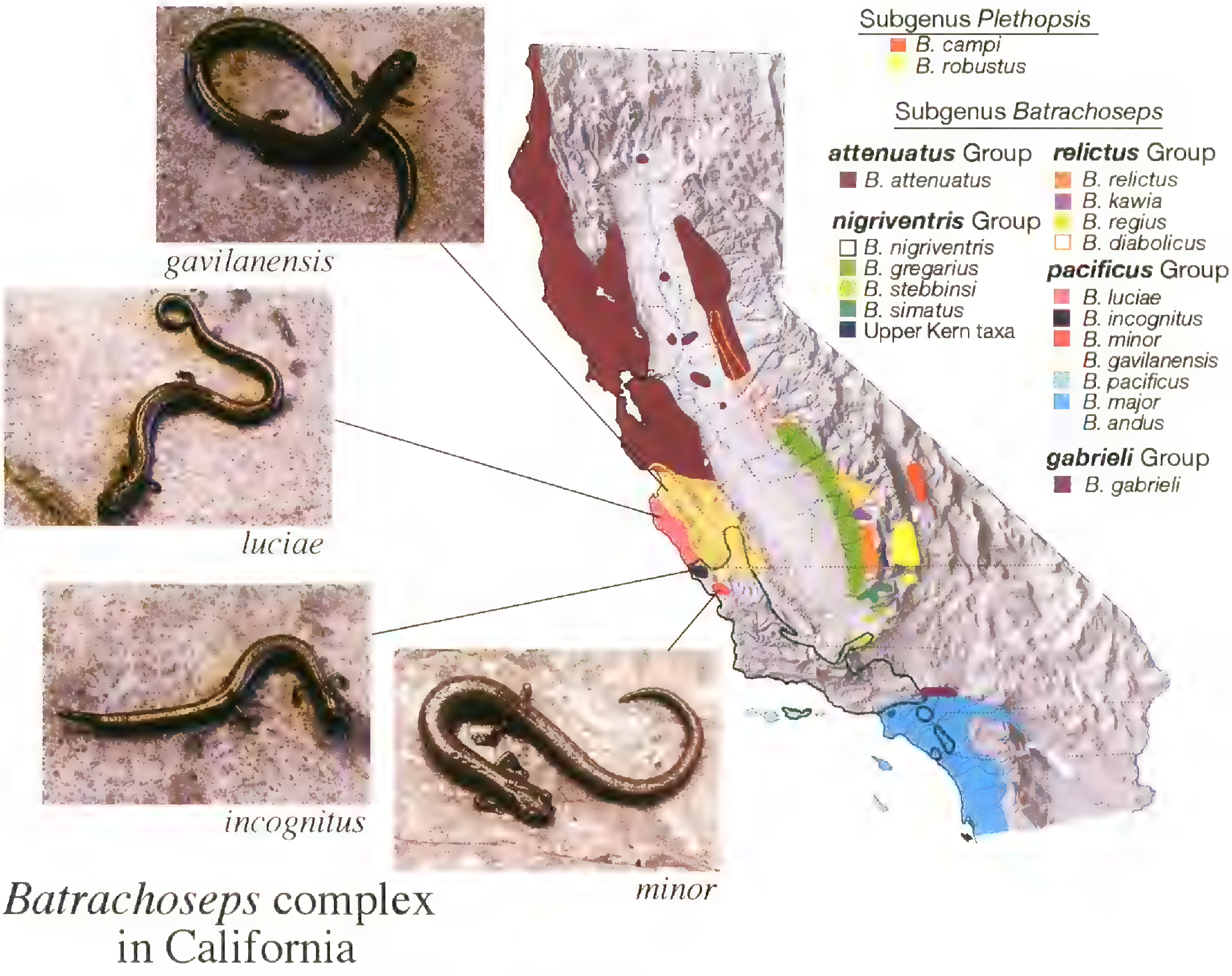


Figure 3. Distribution of the species of *Batrachoseps* in California. The photographs are of specimens of the four species comprising the central coastal cluster of the *pacificus* clade (photos by M. García-París & D. B. Wake). Authorities for species where not provided in the text: *B. campi* Marlow, Brode & Wake, 1979, *B. robustus* Wake, Yanev & Hansen, 2002, *B. kawia* Jockusch, Wake & Yanev, 1998, *B. regius* Jockusch, Wake & Yanev, 1998.

again they replace one another from north to south (Wake & Jockusch, 2000), this pattern apparently continuing into Baja California (unpublished).

These patterns raise questions concerning species delimitation and circumscription. Because *Batrachoseps attenuatus* (*attenuatus* clade) occurs in sympatry with *B. gavilanensis* Jockusch, Yanev & Wake, 2001 (*pacificus* clade) without evidence of interbreeding and with great genetic divergence between them (D as defined in Nei, 1972, ca. 1.6), two species are present, even though they cannot be distinguished in the field. Other instances of sympatry led Brame and Murray (1968) to undertake a progressive revisionary study that was a prelude to subsequent research. Brame and Murray recognized two species in southern California (*B. major*, on the mainland and southern Pacific Islands, and *B. pacificus* Cope, 1865, on the northern Channel Islands), which they separated from *B. attenuatus* on morphological grounds. They also described three species from the southern Sierra Nevada (*B. stebbinsi*, *B. simatus* Brame & Murray, 1968, and *B. relictus* Brame & Murray, 1968). The curious distribution of *B. relictus* (Sierra Nevada, central Coastal California, Santa Cruz Island, and mountains of Baja California) stimulated Yanev (1978, 1980) to conduct an extensive study of allozymes. She found unexpectedly large divergences and high levels of variation within the taxa she recognized. Yanev found that *B. attenuatus* was restricted to the region north of Monterey Bay. In the central coastal region, populations that Brame and Murray considered to be *B. attenuatus* were assigned to *B. pacificus* (an unnamed semispecies, now *B. gavilanensis*). Populations from more southerly parts of the central coastal region identified as *B. relictus* by Brame and Murray were considered by Yanev to constitute another unnamed semispecies of *B. pacificus* (now three species: *B. luciae* Jockusch, Yanev & Wake, 2001, *B. incognitus* Jockusch, Yanev & Wake, 2001, and *B. minor* Jockusch, Yanev & Wake, 2001). Brame and Murray's *B. major* and *B. pacificus* were also considered semispecies by Yanev and treated taxonomically as subspecies of *B. pacificus*. Yanev had a narrower perspective on *B. relictus* (restricted by Yanev to the

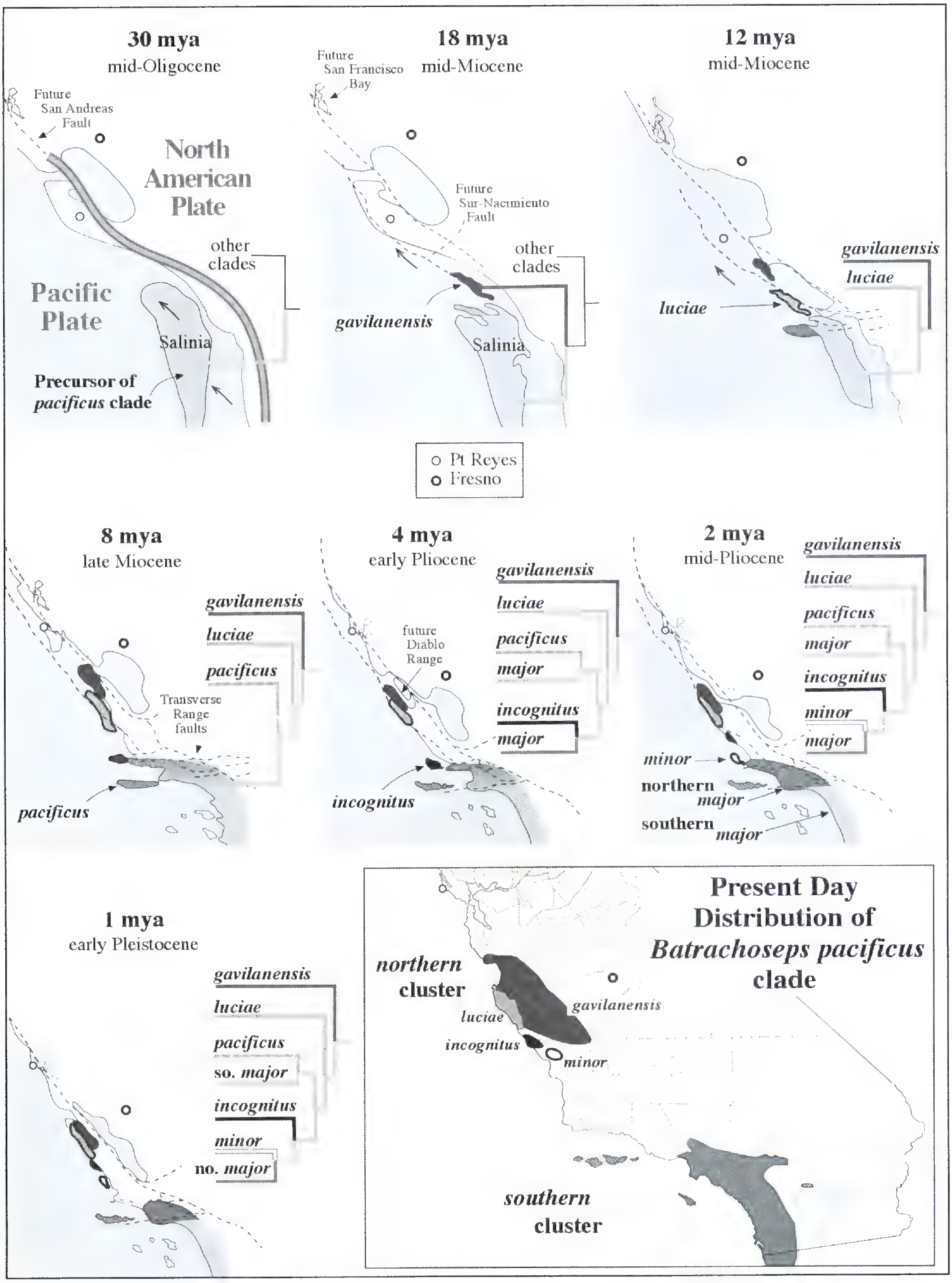


Figure 4. Historical biogeography of the *Batrachoseps pacificus* clade in southern and central California. This scenario is based on geological reconstructions by Hall (2002) and the phylogenetic hypotheses of Jockusch et al. (2002) and Jockusch and Wake (2002).

southern Sierra Nevada), considered to be a semispecies within the *pacificus* complex, and she reduced it, too, to subspecific status. The populations from the mountains of Baja California were considered to represent a final unnamed semispecies of *B. pacificus*. Populations on Santa Cruz Island, assigned to *B. relictus* by Brame and Murray, were assigned by Yanev to a resurrected species, *B. nigriventris* Cope, 1869. In many ways Yanev's recognition of *B. nigriventris* was her most important contribution. This widespread species occurred in sympatry with other species of *Batrachoseps* in central and southern coastal California, on Santa Cruz Island, and in the southern Sierra Nevada. It turned out to be the key in unraveling the complex history of the genus, which is more complicated than even Brame and Murray had conceived. Of special interest was the complex pattern of range overlap with no sign of hybridization or genetic leakage of morphologically cryptic species in the Inner Coast Range in central California, where *B. attenuatus* and the current *B. gavilanensis* were narrowly sympatric in the north, and *B. gavilanensis* and *B. nigriventris* were narrowly sympatric in the south. In coastal central California the geographic range of *B. attenuatus* overlaps that of *B. gavilanensis*, whose range abuts that of *B. luciae*. Parapatry, but as yet with no range overlap, occurs further south between *B. luciae* and *B. incognitus*, and *B. incognitus* and *B. minor* (Figs. 3, 4). However the range of *B. nigriventris* overlaps that of both *B. incognitus* and *B. minor*, with local sympatry, and the northwestern-most range limit of *B. nigriventris* is within a few km of the southern-most range of *B. luciae*.

The addition of mitochondrial gene sequences and the reinterpretation of unpublished data gathered by Yanev (1978), as well as recent discoveries in the field, led to further taxonomic revision (e.g., Marlow et al., 1979; Wake, 1996; Jockusch et al., 1998, 2001; Wake et al., 2003), summarized by Jockusch and Wake (2002). The distribution of species and the inferred pattern of species formation is what Gittenberger (1991) termed nonadaptive radiation, phylogenetic diversification not accompanied by adaptation into distinctively different ecological niches (see also Wiens, 2004, who refers to ecological niche conservatism). The result is a group of allopatric or parapatric species, with the parapatric forms isolated geographically because of inferred competitive interactions at borders of species ranges. The levels of genetic divergence are sufficient to preclude interbreeding or hybridization, and the ecological similarities are sufficient to maintain largely exclusive distributions.

A general feature of the nonadaptive radiation in *Batrachoseps* is the relatively limited sympatry. The only sympatry between two members of any one of the six major clades is between *B. nigriventris* and *B. stebbinsi*, which co-occur in the Tehachapi Mountains at the southern end of the Central Valley. These species display morphological and ecological divergence, unusual among close relatives in this genus. The smaller and more slender *B. nigriventris* is a habitat generalist, found in woodlands under small to large cover objects and using retreats in the soil. The substantially larger and more robust *B. stebbinsi* is most frequently found in rocky soil and small talus slopes. These two species, which are not sister taxa, may have undergone character displacement, and if so it is unique in the genus.

There are some important exceptions to the general rule in *Batrachoseps* that species either replace one another without hybridizing or are sympatric. In southern California, where population density is low, populations of "northern" and "southern" *B. major* that are morphologically identical have mtDNA (cyt *b*) genes that are about 9% diverged and are not sister (Wake & Jockusch, 2000). In fact, mtDNA of southern *B. major* is more closely related to *B. pacificus*, a more robust species that is morphologically distinct, than to northern *B. major* (Fig. 4). However, northern and southern populations are only slightly differentiated in proteins, and Wake and Jockusch argue that when they meet secondarily and interact genetically, alleles from northern populations spread over southern populations, but the interactions have been insufficient as yet to dislodge the maternally inherited southern mitochondrial genes. This situation is reminiscent of *Ensatina e. platensis* in the central and northern Sierra Nevada (see above).

The apparently nonadaptive radiation of *Batrachoseps* results from the complicated geological history of California (Yanev, 1980; Jockusch et al., 2001). The first split, an ancient one, was between members of subgenus *Plethopsis* and subgenus *Batrachoseps*. Today *Plethopsis* is located peripheral to *Batrachoseps*, to the north and east of the main range. Within subgenus *Batrachoseps* the first split segregated *B. attenuatus* from everything else. The *attenuatus* clade, with a single but differentiated species, is distributed mainly northeast of the San Andreas Fault zone and north of the historically significant embayment of the Central Valley in the vicinity of present-day Monterey Bay. The *relictus* clade, perhaps the next to branch phylogenetically, is restricted to the Sierra Nevada and western adjacent lowlands. It displays a distinct pattern of regional displacement, with substantially more divergence than within the *attenuatus* clade. Four species are recognized, each occupying an exclusive geographic range. The northern species, *B. diabolicus* Jockusch, Wake &

Yanev, 1998, split from the remaining species in the vicinity of the mid-Sierran glacial region, a region in which there are north-south splits in diverse taxa. The remaining clades, *gabrieli*, *nigriventris*, and *pacificus*, are largely southern, with *gabrieli* isolated in the southern transverse ranges, *nigriventris* concentrated in the southern Sierra Nevada, Tehachapi Mountains, and some more southerly and westerly extensions, and *pacificus* located in coastal regions, extending from northern Baja California to just north of Monterey Bay, south and west of the San Andreas Fault zone.

The only clade that crosses the San Andreas Fault zone to any degree of significance is *nigriventris*, and in particular *Batrachoseps nigriventris*, a species that has violated the range exclusiveness so characteristic of the genus to establish populations sympatric with members of the *pacificus* clade along the central and southern California coast and on the Channel Islands. This taxon displays greater ecological breadth than any other member of the genus and likely represents an extensive and relatively recent range expansion from its origin, inferred to be near the southern end of the range of its sister taxon, *B. gregarius* Jockusch, Wake & Yanev, 1998, in the vicinity of the Kern River, where so much of the evolution of the *nigriventris* and *relictus* clades has been centered.

The *pacificus* group has been more affected by the massive land movements that have taken place west and south of the San Andreas Fault zone than any of the other *Batrachoseps*. The scenario developed by Jockusch et al. (2001), based on their mtDNA phylogeny, envisioned an origin of the lineage in southern California. A new geological reconstruction of coastal California (Hall, 2002) has enabled a further development of the scenario (Fig. 4). The first split separated the *pacificus* clade from a *nigriventris* or *gabrieli* ancestral sister taxon, with the *pacificus* clade associated with the Pacific geological plate in the paleoterrane known to geologists as Salinia. This may have occurred as long ago as about 30 million years. Since Oligocene, extensive land movements have transported pieces of the continental crust associated with Salinia more than 160 km to the northwest. The first split within the *pacificus* clade was associated with early stages of the northwestward movement and fragmentation of Salinia. Today the northernmost member of the *pacificus* clade, *B. gavilanensis*, is the only species to have penetrated territory north of the ancient Central Valley embayment, in the vicinity of present-day Monterey Bay. Its penetration northward, probably a relatively recent event, has established a zone of sympatry with *B. attenuatus*. As one would expect for a relatively old species, *B. gavilanensis* shows the greatest degree of protein and mtDNA diversity within the northern cluster of extant species in the *pacificus* clade.

The next species to split (Fig. 4) was present-day *Batrachoseps luciae*, which now occurs on a plate fragment (Jockusch et al., 2001). After the first two splits our phylogeny is less robust. What is clear is that each of the central coastal species is sister not to its nearest geographic neighbor but to some complex of populations to the south. Thus, *B. pacificus* appears to have been the next to move north, and out to sea, on the precursor terrane that gave rise to the northern Channel Islands, becoming isolated from populations on the mainland. Progressively, *B. incognitus* and *B. minor* were transported northward, leaving a complicated *B. major* in the south that is made up of several distinctive phylogeographic units, essentially left over from episodes of isolation. The northern phylogeographic unit within *B. major* either has or is in the process of extending its range south and east, where it appears to be merging genetically with populations characterized by non-sister mtDNA haplotype clades, morphology, or both. For example the problematic *B. aridus* Brame, 1970, variously recognized as a subspecies of *B. major* or as a full species, is closely related to a southern phylogeographic unit of *B. major*.

The *pacificus* clade displays at a fine scale what I consider to be a long-sustained pattern of nonadaptive radiation in *Batrachoseps*. An ancient lineage fragmented again and again, with a resulting patchwork-quilt pattern of lineage segments, i.e., species, that generally show "tight stitching," close parapatry with no hybridization. Some restricted sympatry occurs between members of different major clades, which in the cases of *B. nigriventris* and *B. gregarius* is more widespread and involves more than one other taxon.

Why the nonadaptive radiation in *Batrachoseps* resulted in a patchwork-quilt pattern of distribution requires closer examination of the history of the central coastal region. The four species of the *pacificus* clade in this region occupy closely abutting geographic ranges, and they are very similar in morphology and ecology (Figs. 3, 4). Two of these, *B. gavilanensis* and *B. luciae*, occupy relatively large areas and have sufficient samples to disclose significant geographic and genetic variation. These two species show extensive geographic variation in both allozymes and mtDNA haplotypes. In fact, the differences within each approach the level of difference between them (Jockusch et al., 2001). Yet, in the border zone where the ranges of the two species abut, no syntopy or genetic interchange is detected. Genetic distances across this border remain high, with some fixed allozymic differences and complete segregation of mtDNA haplotypes, but no ecological differentiation is observed.

The patchwork pattern, which is general in the genus, likely arises from several factors. First, these salamanders are extremely sedentary, with limited dispersal. Second, today's species represent lineage fragments of former species, which themselves were geographically differentiated. Thus species are "born" with geographic variation. Third, species, especially close relatives within a clade, replace one another geographically because they are so similar ecologically that there is what may be called preemptive occupancy of space. That is, the space-holders have relatively large and well-established populations that resist invasion by others that are virtually identical ecologically. Wiens (2004) has discussed such niche conservatism and considers it to be a major factor in the formation of similar species under allopatric conditions. Areas where populations merge with others having non-sister haplotypes typically are ecologically marginal, with populations scattered and small. Under such circumstances, populations may have very low densities, and individual organisms that meet may have few mating opportunities other than with heterospecific individuals.

Sympatry between species is found in two contrasting situations. The first is where there is some ecological divergence, often related to differentiation in the body sizes of the two species. Examples include *Batrachoseps major* with *B. nigriventris*, *B. nigriventris* with *B. stebbinsi*, and *B. nigriventris* with *B. gabrieli* Wake, 1996. The second is in areas where the ranges of species become discontinuous and where populations are highly localized. This is the situation in the generally inhospitable Inner Coast Range, a largely treeless area with exceedingly hot and dry summers and little winter rain. Here broad regional ranges overlap, but little or no local syntopy is found, as in the cases of *B. attenuatus* and *B. gavilanensis* and *B. gavilanensis* and *B. nigriventris*. This is the same ecological situation in which genetic mergers may take place. One can only speculate that the interactors that fail to merge have been separated sufficiently long (as estimated from allozymic genetic distances and degree of haplotype divergence) that genetic isolating mechanisms have arisen incidental to diverse genetic processes during the long period of geographic isolation.

The main feature of a nonadaptive radiation, then, is the general impression of allopatry or parapatry with a lack of ecological or any other kind of divergence other than in molecular traits. In situations like this, where there is little or no hybridization, it may be fruitful to investigate the evolution of isolating mechanisms, which might have arisen incidentally in allopatry but serve now to cause individuals from adjacent populations not to recognize each other as potential mates. In the case of salamanders, this is most likely to involve mating pheromones (Houck & Arnold, 2003). Postulated premating isolating mechanisms might be incidental, a byproduct of the different genetic histories of lineages since time of divergence. If isolating mechanisms did arise at the borders of two incipient species, it is very difficult to imagine a scenario in which they would spread "backwards" throughout the far-flung populations of each species, which are so genetically heterogeneous. In such situations the evolution of isolating mechanisms seems unlikely to be related directly to the formation of species.

General Discussion

The contrast between *Batrachoseps* and *Ensatina* is great. Where morphologically and ecologically similar populations of *Ensatina* meet they exchange genes, whereas in *Batrachoseps* they do not. Why does this stark contrast exist? The two genera belong to the same major clade (Plethodontidae), have similar life histories and ecologies, and species of the two are often sympatric. Both are fully terrestrial. However, *Ensatina* is a larger salamander, with better locomotory ability and larger home ranges (compare Stebbins, 1954, and Staub et al., 1995, with Cunningham, 1960, and Hendrickson, 1954). Both genera are phylogenetically isolated, having no close relatives, and likely represent very old lineages (perhaps on the order of 60 million years or more, based on estimates from rates of albumin evolution and degree of divergence in mtDNA and other data, e.g., Larson et al., 1981, 2003; Chippindale et al., 2004; Mueller, 2005; Mueller et al., 2004). *Batrachoseps* is the more internally diverged and differentiated, and is likely the older. Its lower vagility, fidelity to pieces of the planetary crust, and inferred great age may be responsible for the fragmentation of the primordial lineage and what has been mainly a nonadaptive radiation. The processes involved in differentiation of *Batrachoseps* appear to be largely related to factors associated with earth history, especially crustal movements, as first proposed by Yanev (1980). In contrast, *Ensatina* appears to be responsive to challenges from its biological community and has evolved several different antipredator mechanisms, which have concomitant behavioral and ecological consequences. The result is a differentiated, but incompletely fragmented and very widespread, metapopulation structure.

Both examples have strong geographic components to their histories. Most species formation in terrestrial vertebrates appears to be geographic in nature, as first generalized by Mayr (1942). Geographic variation

within living terrestrial vertebrate species (as well as many other taxa) in natural populations is nearly ubiquitous (e.g., Avise, 2000). In the taxa I study, there is so much divergence within species that only adaptively significant alleles or allele complexes are likely to spread broadly and rapidly. Accordingly, *Ensatina* has experienced spread of adaptively significant traits, and this has kept the lineage from permanent fragmentation. However, in *Batrachoseps*, where no clearly adaptive traits beyond those general to most species have been identified, divergence and lineage fragmentation has proceeded. To focus attention on the evolution of isolating mechanisms in situations like this is problematic. When long-separated populations that have diverged significantly come into secondary contact they may be sufficiently distinct that they no longer recognize each other as potential mates (e.g., Kozak, 2003). I suspect that this has happened in *Batrachoseps*, where one never finds hybrids, but instances of haplotype paraphyly and polyphyly are found, suggesting that secondary contact was followed by genetic merger (cf. Funk & Omland, 2003). Alternatively, offspring produced in such contacts may be adaptively inferior. This is the case in the adaptively different *Ensatina* in the central Sierran and southern California hybrid zones, which are only a few home-range diameters wide. One might study isolating mechanisms in these instances, but genetic isolation likely evolved incidentally during the allopatric divergences, not upon recontact. Perhaps hybrid zone or alloparapatric interactions (Alexandrino et al., 2005) are settings in which the potential reinforcement of isolating mechanisms might be studied (Servedio & Noor, 2003). Geography is the common theme, whether species formation has progressed adaptively or has been incidental to events related to isolating mechanisms.

At what level of lineage segmentation do we recognize and name species? Recently de Queiroz (2005) pointed out that while the process of evolutionary divergence leads to the acquisition of different properties by diverging lineages, taxonomists differ with respect to which particular property they emphasize. He argues that the adoption of different thresholds is the main cause of the "species problem." I have attempted to use the same thresholds for the two examples presented here, but have reached very different conclusions. De Queiroz argues that "all separately evolving metapopulation lineages would be species" regardless of particular attributes, but in the case of *Ensatina*, for example, the issues of separateness and metapopulation limits remain unclear. The likelihood that once separate lineage segments are now genetically merged, or have in the recent past undergone secondary genetic merger, is high. In contrast, in *Batrachoseps* the same issues are more generally resolved.

Biologists will continue to have problems with species. We may all share the same conceptual framework, but it is safe to predict that arguments concerning thresholds and attributes will continue to produce controversy. However, regardless of taxonomic treatment, careful analysis of patterns and processes associated with species formation will inform meaningful discussion and debate.

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ADAPTATION, SPECIATION, AND CONVERGENCE: A HIERARCHICAL ANALYSIS OF ADAPTIVE RADIATION IN CARIBBEAN *ANOLIS* LIZARDS[1]

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Abstract

Caribbean *Anolis* lizards are a classic case of adaptive radiation, repeated four times across islands of the Greater Antilles. On each island, very similar patterns of evolutionary divergence have occurred, resulting in the evolution of the same set of ecological specialists—termed ecomorphs—on each island. However, this is only part of the story of the Caribbean anole radiations. Indeed, much of the species diversity of Caribbean *Anolis* occurs within clades of ecomorphs, which contain as many as 11 ecologically-similar species on a single island. We ask to what extent the classic model of ecological interactions as the driving force in adaptive radiation can account for this aspect of anole evolutionary diversity. Our answer is that it can in part, but not entirely. More generally, the most complete understanding of evolutionary diversification and radiation is achieved by studying multiple hierarchical evolutionary levels from clades to populations.

Key words: adaptive radiation, *Anolis*, Caribbean, ecomorphs, lizard, speciation.

Adaptive radiation is "evolutionary divergence of members of a single phylogenetic line into a variety of different adaptive forms" (Futuyma, 1998). Models of adaptive radiation (Simpson, 1953; Schluter, 2000) begin with a species in an environment in which resources are plentiful, but few, if any, other species are present to use them. Such a situation could occur in a number of ways, such as colonization of a new area, evolution of a trait that allows the species to use resources previously inaccessible to all species, or surviving a mass extinction. Through time, two things happen: species proliferate and resources become limiting. In some scenarios, speciation occurs first and only later do resources become limiting—this seems to be the model Simpson (1953) had in mind. Alternatively, in other models, resource limitation occurs first, thus driving speciation (e.g., Orr & Smith, 1998; Dieckmann & Doebeli, 1999). In either case, however, the main point is clear: species (or subpopulations of one initial species) alter their behavior and habitat use to partition resources, minimizing competitive interactions. Over time, the species (or subpopulations) evolve features to increase their adaptation to their new niches (i.e., character displacement occurs). In this scenario, multiple, possibly simultaneous, instances of character displacement ensue. The end-result is that a single species has given rise to a number of species each adapted to a different part of the environment—i.e., an adaptive radiation.

Both the definition of adaptive radiation and these models say nothing about the species richness of an adaptively-radiating clade. Indeed, such clades may not be rich in species, despite their ecological and phenotypic disparity. Examples of adaptive radiations with unexceptional species richness include Darwin's finches (Grant, 1986), pygopodid lizards (Webb & Shine, 1994; Jennings et al., 2003), and postglacial lake fish (Schluter, 1996). Nonetheless, many other adaptive radiations—e.g., Rift Lake cichlids (Verheyen et al., 2003), passerine birds (Lovette & Bermingham, 1999), Hawaiian silverswords (Baldwin, 1997)—exhibit not only great ecological and phenotypic disparity, but also exceptional species richness. This species richness is generally not obtained by adaptation to an extraordinary variety of different environments, but rather by the existence of sets of species that are ecologically similar, with each set adapted to a different part of the environment. Understanding the genesis and maintenance of this diversity obviously requires a more complicated model than the simple model of speciation and character displacement just discussed.

The goal of this paper is to examine one species-rich adaptive radiation, Caribbean lizards in the genus *Anolis* Daudin, 1802. By doing so, we hope, first, to

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explore whether the classic model of adaptive radiation can adequately explain the ecological diversification of Caribbean anoles and, second, to examine the determinants of the great species richness of this radiation and investigate whether these determinants are related to the patterns of adaptive differentiation.

The Evolutionary Radiation of Caribbean Anoles

The lizard genus *Anolis* is one of the largest genera of vertebrates (and the largest of amniotes), with well over 300 described species, 154 of which occur on islands in the Caribbean (Nicholson et al., 2005). Of particular interest are the anole faunas of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico). On each of these islands, typical communities contain a number of species, each of which is morphologically distinct, behaves differently, and uses a different part of the structural habitat (e.g., on broad surfaces near the ground, on twigs, in grassy areas). Detailed functional and behavioral analyses support the hypothesis that the morphological differences between the species—in traits such as hindlimb length and toepad size—are adaptations to the functional demands imposed by living in different parts of the environment (e.g., Irschick et al., 1996; Larson & Losos, 1996; Elstrott & Irschick, 2004).

The most striking aspect of this diversity, however, is its repeated occurrence across all four Greater Antillean islands. For the most part, the same set of habitat specialists—termed "ecomorphs" and named for the part of the habitat in which they are usually found (Williams, 1972, 1983)—recurs on each island. In all, there are six ecomorphs: trunk, trunk-crown, trunk-ground, grass-bush, twig, and crown-giant. Four are found on all four islands, whereas grass-bush anoles are absent from Jamaica and trunk anoles are only found on Cuba and Hispaniola. Phylogenetic analysis of morphological and molecular data confirms Williams's pre-cladistic conclusion (1972, 1983) that the ecomorphs are independently derived on each island (Losos et al., 1998; Poe, 2004).

Two aspects of the ecomorph story have received relatively little attention in the years since Williams (1983) classic review. First, the ecomorphs are represented on each island, not necessarily by a single species, but sometimes by many. At the extreme, there are 14 trunk-ground and 15 grass-bush species on Cuba. All ecomorph types are represented by more than one species on at least one island, and at least two trunk-ground and trunk-crown species are present on all islands (Table 1).

Second, in addition to the ecomorphs that have evolved repeatedly on different islands, a number of

Table 1. Numbers of *Anolis* species of each ecomorph type on each island in the Greater Antilles.

	Cuba	Hispaniola	Jamaica	Puerto Rico
Crown-giant	6	3	1	1
Grass-bush	15	7	0	3
Trunk	1	6	0	0
Trunk-crown	5	4	2	2
Trunk-ground	14	9	2	3
Twig	5	4	1	1
Other/unique	12	8	1	0
Total	58	41	7	10

habitat specialists have evolved on only one island. These "unique" types include the semi-aquatic streamside *Anolis vermiculatus* Duméril & Bibron, 1837 on Cuba, the rock wall specialist *A. bartschi* Cochran, 1928 on Cuba, and the leaf-litter specialist *A. (Chamaelinorops) barbouri* Schmidt, 1919 on Hispaniola, among others. In some cases radiation has occurred subsequent to the evolution of such specialists; for example, four large species on Cuba (formerly comprising the genus *Chamaeleolis* Cocteau, 1838) are particularly slow-moving species specialized for narrow perches high in the canopy, and may prefer to feed on molluscan prey (Leal & Losos, 2000). All told, 21 such unique specialist species exist, 12 on Cuba, 8 on Hispaniola, 1 on Jamaica, and none on Puerto Rico (Table 1).

Molecular Phylogenetic Perspective

Recent molecular studies have provided a phylogeny for most of the species in the entire Caribbean radiation (Jackman et al., 1999, 2002; Creer et al., 2001; Schneider et al., 2001; Glor et al., 2003, 2005; Harmon et al., 2003; Brandley & de Queiroz, 2004; Poe, 2004). The most recent phylogeny (Nicholson et al., 2005), based on sequence from a 1.8 kb region of mitochondrial DNA for 132 of the 154 Caribbean species, provides the ability to thoroughly examine the Caribbean anole radiation, including both ancient events deep in the tree and many of the more recent divergences. This examination reveals three patterns of interest that characterize anole evolutionary diversification in the Greater Antilles (Fig. 1):

(1) Ecomorphs have generally evolved only once on each island. Given that each ecomorph has evolved on multiple islands and that multiple representatives of each ecomorph type are present on most islands, one might predict that ecomorph types have evolved more than once within islands. The phylogeny, however, reveals this not to be the case. Most ecomorphs have

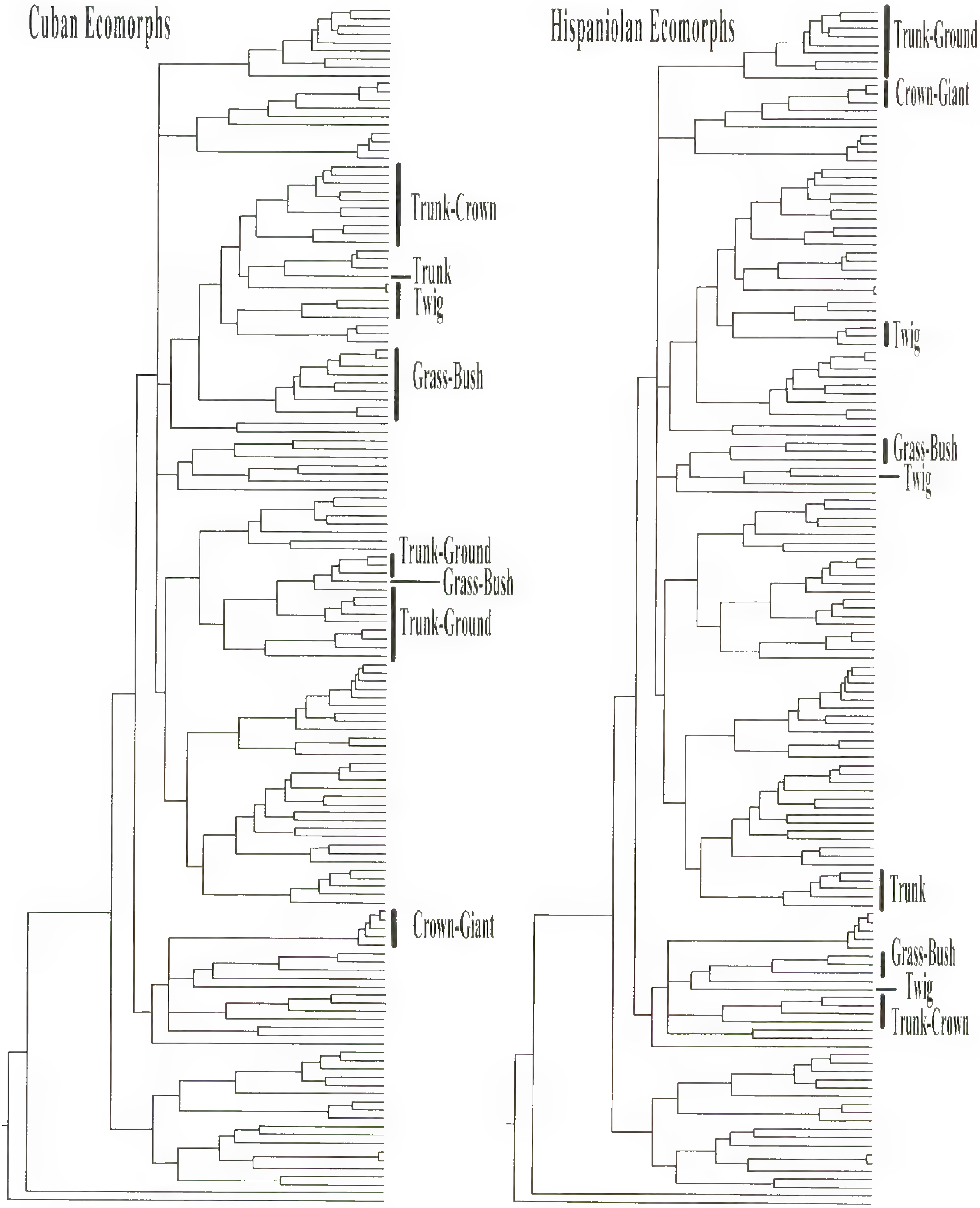

Figure 1. Island-by-island examination of the evolution of habitat specialization in the Greater Antilles. Anole phylogeny from Nicholson et al. (2005); branch lengths made ultrametric using penalized likelihood (Sanderson, 2002). Penalized likelihood was implemented using the program r8s (Sanderson, 2003). The smoothing parameter was 0.90, and branch lengths were scaled to relative time by assigning the root node an arbitrary age = 100. All Central and South American branches were subsequently pruned out using the program TreeEdit (Rambaut & Charleston, 2001). Terminal taxon names were removed for conciseness, but may be viewed, along with the tree file, online at <http://biology4.wustl.edu/~lososlab/anolis_mbg_2005/>. Ecomorph designation is based on previous analyses or, for some newly described species, represents new interpretations based on the species' description. In a few cases (Losos & de Queiroz, 1997; Glor et al., 2005), ecomorph species occur on nearby islands (e.g., the trunk-crown *carolinensis* group in Cuba also contains ecomorphologically similar species in the Bahamas, Little Cayman, Navassa, and Florida). In the figure, these species are included with their Greater Antillean relatives (i.e., all *carolinensis* group species are indicated as Cuban trunk-crown anoles).

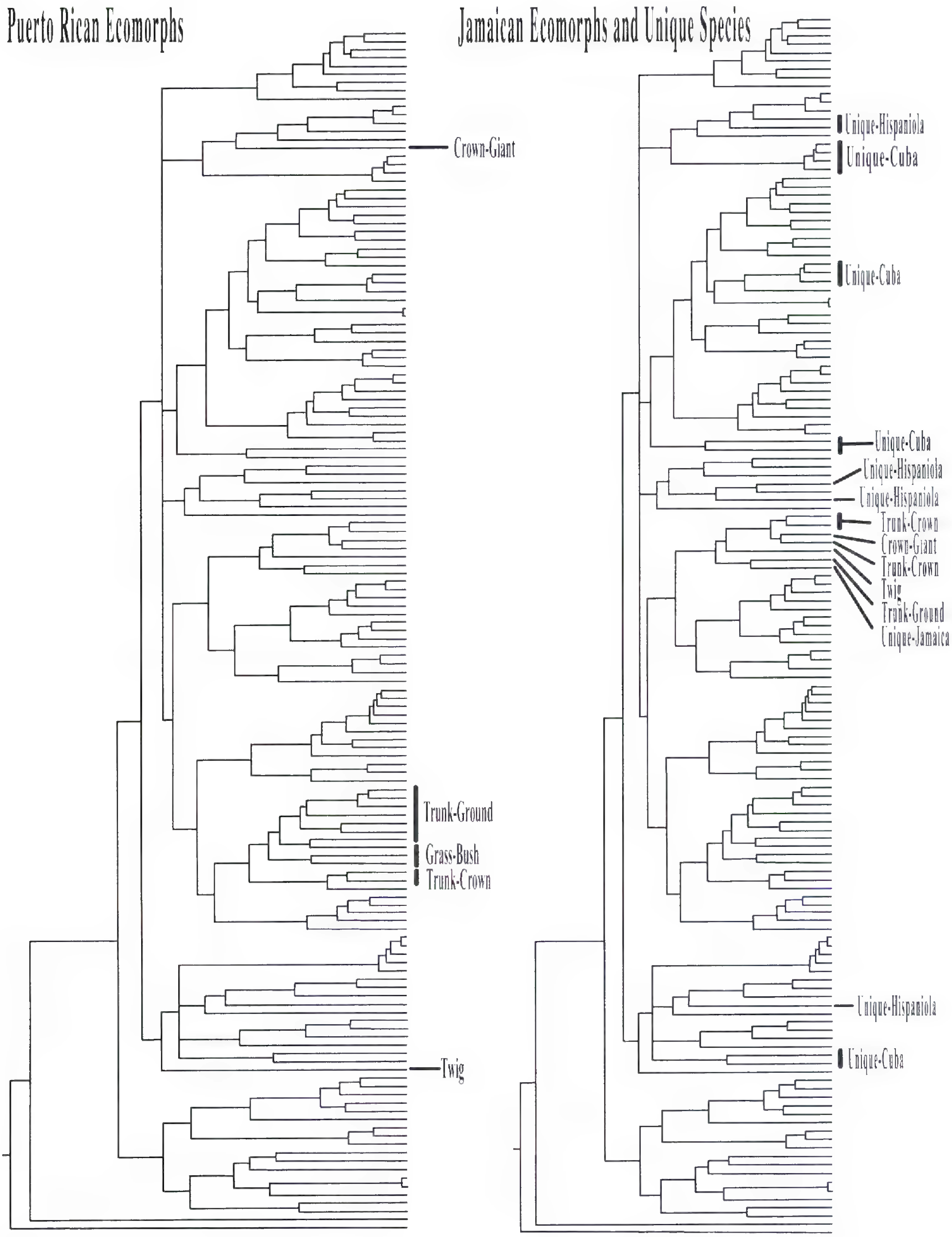

Figure 1. Continued.

evolved only a single time on an island, though evidence exists for two instances of evolution of twig and grass-bush anoles on both Cuba and Hispaniola (however, a phylogeny in which the two twig lineages in Cuba are sister taxa, implying a single origin, is almost as well-supported as the phylogeny in Fig. 1). In addition, either trunk-ground or grass-bush anoles have evolved twice on Puerto Rico (the nested position of the trunk-ground *Anolis gundlachi* Peters, 1876 within a clade of grass-bush anoles makes distinguishing between the two possibilities difficult; see Brandley & de Queiroz, 2004) and trunk-crown anoles

may have evolved twice on Jamaica (alternatively the crown giant *A. garmani* Stejneger, 1899 may have evolved from an ancestral trunk-crown anole).

(2) Ecomorphs are generally not phylogenetically nested within other ecomorphs. With few exceptions (e.g., the grass-bush anole, *Anolis ophiolepis* Cope, 1862, which arose from within a clade of Cuban trunk-ground anoles [Fig. 1] and the two other cases mentioned above), most ecomorph clades are monophyletic and do not give rise to other ecomorphs. The "unique" habitat specialists also rarely, if ever, arise from within a clade of one of the ecomorphs (Fig. 1; one possible exception is ambiguous: two Hispaniolan unique anoles, *A. eugenegrahami* Schwartz, 1978 and *A. christophei* Williams, 1960, form a clade with the clade of Hispaniolan crown-giants; in turn, the sister taxon to this clade is the Puerto Rican crown-giant *A. cuvieri* Merrem, 1820).

(3) Ecomorph and "unique" habitat specialist clades are old. Examination of Figure 1 indicates that almost all ecomorph clades arose in the first half of anole evolutionary history on most islands (the exception is Jamaica, the short branches of which support suggestions that Jamaica was underwater until well into the Miocene; but see Hedges, 2001). But how old does that make them in absolute terms? Very old, according to several lines of evidence. First, if one accepts clock-like evolution of the mtDNA region examined, the maximum pairwise difference among species exceeds 40% (after correction for multiple substitutions), which suggests evolutionary divergence more than 30 million years ago (based on calibration from Macey et al., 1998). Second, microcomplement fixation, an independent molecular clock estimation based on divergence in albumin proteins, provides a very similar estimate for the earliest divergence within *Anolis*, 35–40 million years (Shochat & Dessauer, 1981). Third, three fossil amber anoles from the Dominican Republic date to the Miocene or possibly older (Rieppel, 1980; de Queiroz et al., 1998; Polcyn et al., 2002). Two of these specimens are whole animals (the third, described by Polcyn et al. (2002) comprises little more than the head) and are morphometrically indistinguishable from extant trunk-crown anoles, indicating that at least one ecomorph clade was present > 20 million years ago (de Queiroz et al., 1998). Moreover, the trunk-crown anoles from Hispaniola, the *chlorocyanus* group, comprise an ancient clade (Fig. 1), and the amber specimens cannot be osteologically distinguished from extant members of this group.

The Role of Ecological Interactions in Driving Anole Diversification

The classic model of adaptive radiation posits that ecological interactions, primarily interspecific competition, drive ecological divergence and adaptation to different parts of the environment (Simpson, 1953; Schluter, 2000). A corollary of this hypothesis, however, would be the prediction that once one species specializes for a particular aspect of the environment, other lineages should have difficulty occupying this niche. This prediction could explain the paradox of ecomorph evolution: repeated evolution across islands, but few instances of multiple evolution within an island. Thus, it would appear that once an ecomorph evolves on an island, it achieves ecological incumbency and prevents other lineages from entering that niche. The inability of introduced species to become invasive when ecologically similar species already occur in an area, in contrast to their invasiveness in areas lacking such species, further supports this prediction (Losos et al., 1993).

The adaptive radiation scenario hinges on the assumption that anoles interact strongly. Indeed, a wealth of data (reviewed in Losos, 1994; Roughgarden, 1995; more recent examples include Leal et al., 1998; Losos & Spiller, 1999; Campbell, 2000) attests to the strength of interspecific interactions among anole species. These studies come in a variety of forms, including experimental manipulations, natural experiments, and comparative ecology. Studies document effects in terms of differences in growth rates, habitat use, reproductive rates, and density. Despite the great variety of study systems and approaches taken, one result is readily apparent: sympatric anole species tend to interact strongly. Review of these studies leads to several conclusions (Losos, 1994): first, the more similar species are ecologically, the stronger are the interactions between them; second, anole species alter their habitat use in the presence of ecologically similar species; and, third, anoles evolve phenotypically in response to shifts in habitat use.

Evolution within Ecomorphs

The evolutionary divergence and stasis of ecomorph types can reasonably be interpreted as the result of interspecific interactions. These interactions, however, also have likely played a role in within-ecomorph differentiation.

When examining diversity within ecomorph clades, several patterns are apparent. First, many species are allopatrically or parapatrically distributed. At least some of these allopatric forms are located in different mountain ranges. The most parsimonious explanation of these distributions is that they reflect the early stages of allopatric speciation: populations that have become isolated and diverged to the point that they are likely to be reproductively isolated. In this context, the use by anoles of their dewlap (an extensible flap of skin located on the throat; Fig. 2) in communication is fortuitous. Sympatric anole species invariably differ in some aspect of dewlap "design" (color, pattern, size); these differences appear to be used as species recognition signals (reviewed in Fleishman, 2000; Losos, 2004). As

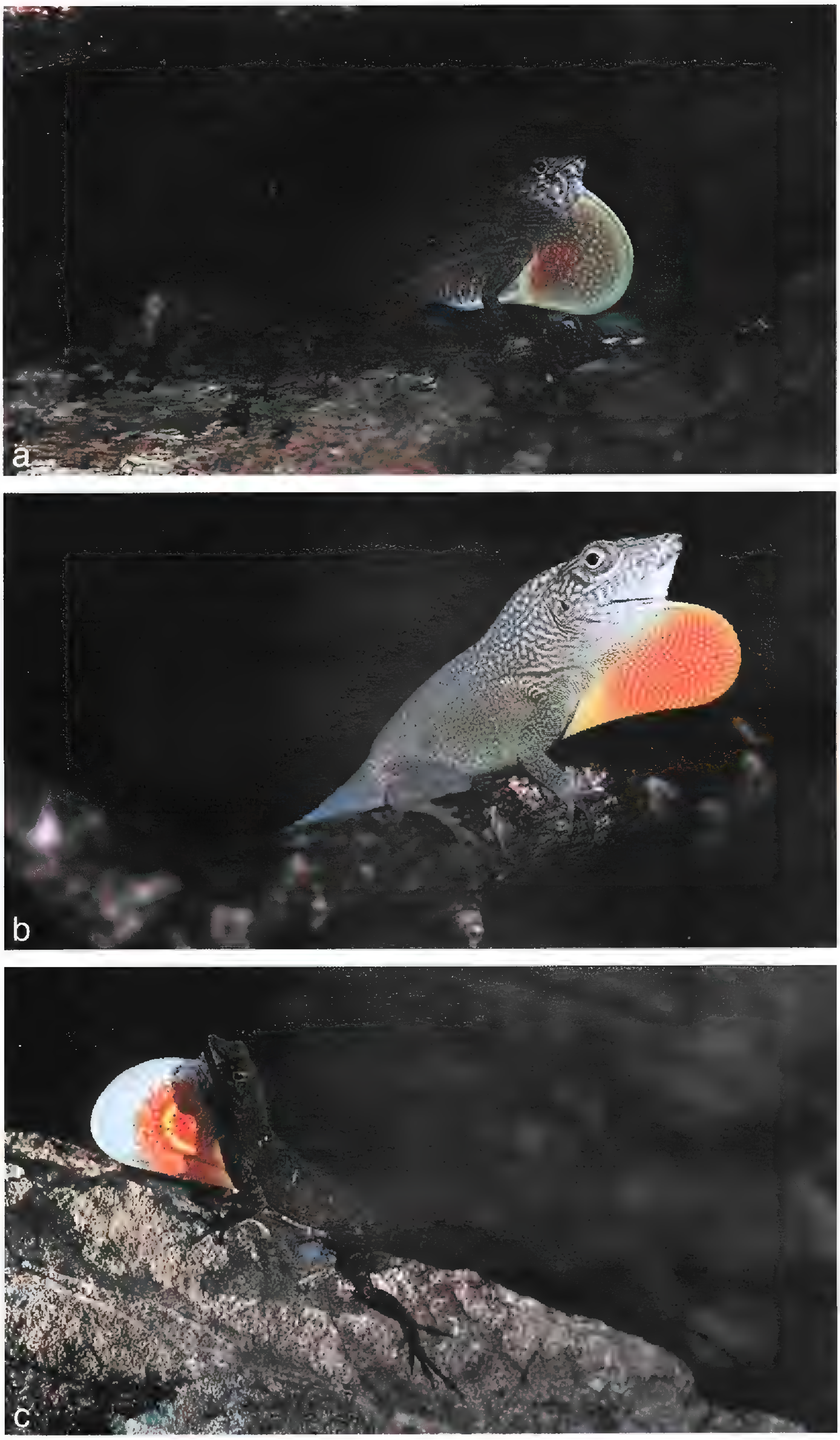

Figure 2. Dewlap diversity in Caribbean anoles. —a. *Anolis allogus* (Barbour & Ramsden, 1919), Cuba. —b. *A. grahami* (Garman, 1888), Jamaica. —c. *A. mestrei*, Cuba.

a result, it is possible to identify allopatrically distributed taxa that are likely to be reproductively isolated in a non-arbitrary way.

Many of these allopatrically and parapatrically distributed taxa (which correspond to the concept of "allospecies" or "semi-species"; Mayr, 1963) appear to be ecologically very similar; that is, they are ecologically equivalent, but occur in different places. Of course, because the ranges of these species are often small and in out-of-the-way places, the ecology of many of these species is poorly known, so this statement must be considered tentative.

Not all of these species are ecologically similar, however. In some cases closely related species have differentiated to adapt to local conditions. For example, members of the *Anolis cybotes* Cope, 1862 group in Hispaniola are adapted to use a variety of different habitat types, such as pine forest, rocky terrains, and semi-deserts (Glor et al., 2003). Moreover, these ecological differences are so great as to permit sympatry in some cases, the extreme of which is the trunk-ground anoles of Soroa, in western Cuba, where four members of the *sagrei* group coexist. All four of these species can be distinguished ecologically by a combination of their thermal and structural microhabitats (one species occurs in hot, open habitats at the forest edge, a second in relatively open areas within the forest, and two in deep forest; the latter two, in turn, differ in their use of boulders within the forest, with one species, *A. mestrei* Barbour & Ramsden, 1916, always found on or near boulders or rock walls; Losos et al., 2003; see also Ruibal, 1961).

More generally, a pattern exists in the ecological means by which closely-related members of the same ecomorph type are able to coexist. In the ecomorphs that occur on or near the ground, the trunk-ground and grass-bush ecomorphs, sympatric species usually differ in thermal microhabitats, as just discussed for Soroa (sympatry of grass-bush anoles in eastern Cuba requires further study; at this point, ecological differences are not known, but few data are available). By contrast, sympatry in the more arboreal ecomorph types (trunk-crown and crown-giant) is correlated with differences in body size, which correlates with prey size (references in Losos, 1994). Thus, sympatric trunk-ground and grass-bush anoles tend to be approximately the same size, but occur in different microclimates, whereas sympatric trunk-crown, twig, and crown-giant anoles tend to be more similar in microhabitat, but differ in body size.

These patterns of ecological divergence in members of an ecomorph class lead to the following scenario: first, speciation occurs in allopatry. The mechanisms contributing to allopatric speciation within islands are poorly understood, but one recent study suggests that fluctuating sea levels and tectonic events have contributed to population fragmentation and allopatric divergence in Cuban trunk-crown anoles (Glor et al., 2004). Most allopatric populations remain ecologically similar (the concept of "niche conservatism"; Webb et al., 2002). This ecological similarity precludes sympatry when allopatric species come into contact, leading in some cases to parapatry. Second, in some instances, allospecies diverge to adapt to their local environments. Third, such divergence sometimes permits sympatry, leading to the coexistence of members of the same ecomorph class, which partition resources along axes other than the structural habitat axis (which is the axis that is partitioned between ecomorphs). An alternative possibility, of course, is that the differences permitting coexistence arise after sympatry (the classic model of character displacement). Although detailed examination of particular cases is required to distinguish these two scenarios, the existence of ecological divergence in allospecies indicates that sympatry is not required to drive divergence.

Within-Species Divergence

Recent studies have added an unexpected new twist to the scenario detailed above. Studies beginning in the mid-1990s on several Lesser Antillean anole species revealed high levels of inter-populational genetic differentiation in mitochondrial DNA (Malhotra & Thorpe, 1994; Thorpe & Malhotra, 1996; Schneider, 1996). Although a number of subspecies had previously been described for some of these species (as many as 12 for *Anolis marmoratus* Duméril & Bibron, 1837 on Guadeloupe; Lazell, 1972), levels of genetic differentiation exceeding 9% uncorrected sequence divergence between geographic haplotype clades were unexpected, particularly for densely populated, mobile organisms such as Caribbean anoles.

Further research, however, reveals that the same pattern is found in Greater Antillean (Jackman et al., 2002; Glor et al., 2003, 2004; Kolbe et al., 2004) and Amazonian anoles (Glor et al., 2001). Ongoing research indicates that extremely high levels of geographic differentiation in mitochondrial DNA may be the norm (R. Glor, unpublished).

These results are exciting for several reasons. First, and most generally, they indicate that, despite 40 years of intensive work on anole evolutionary ecology, one aspect of anole diversity has been overlooked. Second, the results suggest the existence of unrecognized evolutionary units, perhaps worthy of recognition as species. As a result, the species diversity of anoles may, possibly, be much greater than previously recognized. Of course, robust diagnoses of morphologically cryptic species will require more than mitochondrial DNA data (Moritz, 1994; Sites & Crandall, 1997). Analyses of variation at a nuclear locus in one Cuban group supports the major intraspecific differentiation identified by mtDNA (Glor et al., 2004), but the same is not true of at least one Lesser Antillean species where the pattern of gene flow inferred from microsatellite data disagrees with that of mtDNA (Stenson et al., 2002). Further work examining other loci is necessary to test

the hypothesis that these forms are genetically distinct.

If these forms are genetically distinct, then what are currently recognized as single, island-wide species in the Greater Antilles may, in fact, be complexes of parapatrically-distributed species. Such parapatry would suggest that the forms are ecologically identical and thus unable to coexist in sympatry. Certainly, ecological differences had not previously been identified for most of these populations, so the hypothesis is reasonable, though requiring further, detailed investigation. Nonetheless, to the extent that the hypothesis is correct, then these recent findings on intraspecific differentiation extend the scenario for differentiation proposed above for semispecies: the first step in differentiation may be the evolution of ecologically similar forms that occur in allo- or parapatry; evidence of these forms comes not only from allopatrically distributed populations recognized as different species, but also by the existence of genetically differentiated populations that are parapatrically-distributed and may be reproductively isolated.

Conclusions

Evolutionary diversification of *Anolis* lizards in the Greater Antilles conforms to our ideas about adaptive radiation. On each island, species have diversified, producing a set of species adapted to different ecological niches. Studies on extant species indicate that sympatric species routinely experience strong ecological interactions, the strength of which is a function of how similar ecologically two species are. Moreover, species alter their resource use in the presence of ecologically similar congeners and, over evolutionary time, evolve adaptations to their altered regime of resource use. In sum, the evidence for ecological interactions as the driving force in adaptive radiation is probably as strong for Caribbean anoles as it is for any other group.

However, this is not the whole story for the Caribbean anole radiation. Many closely-related species are ecologically similar, but not sympatric. Ecological divergence appears to play little role in the speciation process of these species (at least ecological divergence that relates to resource partitioning among sympatric species; see Losos, 2004). Moreover, some of these semispecies have diverged ecologically to adapt to the particular environment in which they occur. Thus, not all speciation is related to ecological divergence, and not all ecological divergence is related to resource partitioning among sympatric species.

Nonetheless, when these closely related species—which occupy the same structural habitat niche and are members of the same ecomorph class—are found sympatrically, they do partition resources. Whether the differences among these species arise prior to sympatry and are a necessary prerequisite for coexistence, or whether they arise after sympatry in the same sort of character displacement process presumably responsible for ecological divergence between the ecomorphs, is not yet clear.

Regardless, these closely related sympatric species indicate that adaptive radiation has occurred within, as well as between, ecomorph classes. At least some, but certainly not all, of the diversity within ecomorphs is the result of the same sort of evolutionary ecological processes responsible, at a deeper phylogenetic level, for evolution of the ecomorphs themselves.

A second message to be taken from the anole story is that adaptive radiations often must be studied at multiple levels: at the level of clades, species, and populations. Only by studying all of these levels can we get the most complete picture of the patterns and processes responsible for evolutionary diversification in Caribbean anoles.

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HYBRID SPECIATION IN WILD SUNFLOWERS[1]

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ABSTRACT

Hybrid speciation refers to the establishment of novel hybrid genotypes that are reproductively isolated from their parental species and genetically stabilized. Most frequently, reproductive isolation is achieved via an increase in ploidy. However, in some instances new hybrid species arise and become reproductively isolated without a change in chromosome number, a process known as diploid or "homoploid" hybrid speciation. The annual sunflowers of the genus *Helianthus* provide a well-studied example of this latter mode of speciation. Here, I review this work, placing individual studies in their proper context. These include (1) computer simulations that describe the evolutionary conditions under which hybrid speciation is most likely; (2) molecular phylogenetic studies that document the origins of three hybrid sunflower species; (3) comparative genetic mapping studies that describe the karyotypic changes associated with hybrid speciation; (4) experimental re-creations of homoploid hybrid species that allow genotypic and phenotypic comparisons between synthetic and ancient hybrid lineages; (5) quantitative trait locus (QTL) studies that describe the genetic basis of phenotypic differences between the parental species and the mode of gene action underlying the generation of extreme phenotypes in hybrids; (6) phylogeographic studies that estimate the ages and number of origins of each hybrid species; (7) selection studies that measure the strength of selection on individual traits and QTLs in synthetic hybrids transplanted into hybrid habitats; and (8) candidate gene studies that search for correlations between candidate genes for ecological divergence and traits and QTLs shown to be under selection in the habitats of the hybrid species. Ongoing work includes searches for the molecular signature of selection during hybrid speciation, surveys of gene expression shifts associated with hybrid speciation, and experiments that evaluate the role of new hybrid gene combinations versus reproductive isolation in the ecological divergence of hybrid lineages.

Key words: ecological divergence, genetic mapping, *Helianthus*, homoploid hybrid speciation, QTLs, reproductive isolation.

Species often come into contact before reproductive barriers are fully formed, resulting in the formation of hybrid swarms or hybrid zones. The consequences of hybridization are most frequently discussed in relation to the reproductive isolation of the hybridizing lineages. That is, the hybrid zones may be stable, reflecting a balance between dispersal and selection (Barton & Hewitt, 1985). Alternatively, they may be ephemeral, due either to the strengthening of reproductive barriers and cessation of hybridization (Noor, 1999) or to the weakening of reproductive barriers and fusion of the hybridizing lineages (Wolf et al., 2001). All of these consequences are well documented empirically, although their frequencies remain poorly understood.

The consequences of hybridization may also be discussed with respect to adaptive evolution (Anderson, 1949; Arnold, 1997). In stable hybrid zones, for example, favorable alleles will move rapidly across hybrid zones, and thereby contribute to adaptation in the recipient species. This "adaptive trait introgression" may be common, but it is difficult to detect because the introgressing alleles will spread rapidly to fixation and are unlikely to be "caught in the act" (Barton, 2001). Less frequently, hybrids may escape from hybrid zones, which allows fit hybrid gene combinations to become established (Buerkle et al., 2000). Although seemingly rare, these stabilized hybrid lineages are much easier to detect and study. As a consequence, much of what we know about the role of hybridization in adaptive evolution comes from the study of these hybrid races or species (Rieseberg et al., 2003).

Finally, a significant component of the literature on hybridization and its consequences has focused on the means by which these new hybrid lineages become reproductively isolated from their parental species. Most commonly, isolation arises as a by-product of hybrid genome duplication or allopolyploidy (Stebbins, 1950). However, reproductive isolation sometimes develops without a change in chromosome number, a mode of speciation called diploid or homoploid hybrid speciation (Grant, 1981).

In this paper, I review a series of studies conducted by my lab over the past 15 years that describe the origins of three diploid hybrid sunflower species, the means by which they became reproductively isolated from their parental species, and the theory underlying the process. This narrative serves several purposes. First, our theoretical and empirical work provide

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convincing evidence that hybridization can contribute to adaptive evolution and suggest that it may sometimes serve as a mechanism for large and rapid evolutionary transitions. Second, the work illustrates the kinds of experiments required to rigorously assess hybridization's role in evolution. Finally, the sunflower hybrid speciation story is currently scattered across the literature, appearing in more than 25 papers. This narrative ties these pieces together, placing individual studies in their proper context.

Hybrid Speciation: Theory

Hybrid speciation refers to the process in which novel genotypes generated by hybridization become isolated from their parental species and other hybrid genotypes and become genetically stabilized. Reproductive isolation is straightforward for hybrids with increased ploidy because hybrids between polyploids and their diploid parents typically have an odd number of genomes and may therefore be largely sterile (Grant, 1981). In contrast, homoploid hybrid speciation represents a challenge to evolutionary theory, because homoploid hybrid lineages must become established despite the possibility of backcrossing with their parental species (Turelli et al., 2001).

Three mechanisms have been proposed by which a homoploid hybrid may become reproductively isolated from its parental species. First, the new hybrid lineage may diverge karyotypically from its parental species through the sorting of chromosomal rearrangements that differentiate the parental species (Stebbins, 1957; Grant, 1981), and/or by the establishment of new chromosomal rearrangements induced by recombination (Rieseberg et al., 1995b). Second, it has been speculated that hybrid founder events may facilitate hybrid speciation by providing initial spatial isolation for the new hybrid lineage (Charlesworth, 1995). Third, a hybrid lineage may colonize a new habitat or niche and thus become ecologically isolated from its parental species (Grant, 1981). Hybrid species often occupy habitats that are very different from those occupied by their parental species (Rieseberg, 1997; Wang et al., 2001; Gross & Rieseberg, 2005). This is probably because a novel hybrid lineage is more likely to survive if it experiences little competition with its parental species and if divergence in habitat preference results in some spatial isolation with the parental species (Templeton, 1981; Charlesworth, 1995).

Three simulation studies have examined the process of homoploid hybrid speciation (McCarthy et al., 1995; Buerkle et al., 2000, 2003). The first of these was a spatially explicit individual-based simulation, which monitored the consequence of hybridization between species that differed in karyotype (McCarthy et al., 1995). There were two possible outcomes—the generation of a stable hybrid zone or the origin of a novel hybrid genotype that displaced the parental species. The latter outcome was considered hybrid speciation, but it probably is more correctly viewed as the merger of species through hybridization. In most documented hybrid species, the parental species continue to coexist with the derived hybrid (Rieseberg, 1997). Thus, our group developed a computer simulation model to investigate the conditions for this more conventional kind of hybrid speciation (Buerkle et al., 2000), which is the focus of this paper. Our model was similar to that of McCarthy et al. (1995) in its inclusion of chromosomal rearrangements, but differed by providing a novel habitat in which hybrids were favored, as well as the possibility of spatial separation between the novel hybrid habitat and that of the parental species.

Three possible outcomes were possible in our model: hybrid zone stasis, hybrid speciation, and adaptive trait introgression, in which one of the parental species colonizes the novel habitat by acquiring advantageous alleles from the other parent. This latter outcome was by far the most common. Hybrid speciation was less frequent, but it did occur at a significant rate when the sterility barrier isolating the parental species was weak and hybrid genotypes were strongly favored in novel, open habitat (i.e., strong ecological selection). In contrast, hybrid zone stasis was rare, apparently because of the presence of novel habitat in which hybrid genotypes had a fitness advantage.

The conditions required for the independent evolution of the new hybrid species following its origin are surprisingly different from those favoring establishment in the first place (Buerkle et al., 2000). Although a weak sterility barrier between the parental species favors speciation, it also translates into an even weaker barrier between the new hybrid lineage and its parents. As a consequence, the genetic integrity of the new hybrid lineage cannot be maintained in parapatry with parental populations. Thus, for hybrid lineages to evolve independently from parapatric parental populations, the initial sterility barrier between the parental species must be strong, a requirement that greatly reduces the likelihood of this mode of speciation. Alternatively, isolation of the hybrid neospecies can be maintained by strong ecological selection and/or spatial isolation, a result that accords well with earlier verbal predictions that hybrid speciation is most likely following hybrid founder events, in which a few hybrids found a new population that is ecologically

and spatially isolated from the parental species (Charlesworth, 1995; Rieseberg, 1997).

The third simulation study (Buerkle et al., 2003) was an extension of Buerkle et al. (2000), except that the novel habitat for hybrids was eliminated, the sizes of the hybridizing parental populations were allowed to vary, and the extent of spatial isolation was reduced. This new model allowed us to assess the relative frequency of the four most important outcomes of hybridization: hybrid zone stasis, hybrid speciation, adaptive trait introgression, and extinction of one of the parental species (typically the rare one). Hybrid zone stasis was most common, occurring in 84% of simulations. Extinction of the rarer species occurred only when the sterility barrier was weak and was essentially always the result of adaptive trait introgression. Hybrid speciation occurred in only 2.1% of the simulations and was favored by a weak sterility barrier between the parental species and moderate to strong ecological selection. However, hybrid speciation was almost always accompanied by extinction of one of the parental species. These results indicate that the presence of novel habitat greatly facilitates hybrid speciation, as has been suggested by numerous students of hybrid speciation over the past century (e.g., Kerner, 1894–1895; Grant, 1981; Templeton, 1981; Arnold, 1997; Rieseberg, 1997). Also, without an open niche, one of the parental species is replaced by the hybrid, and total species diversity remains unchanged.

All three simulations studies have one remarkable result in common. When hybrid speciation does happen, it occurs quickly, often in fewer than fifty generations. Thus, McCarthy et al. (1995) referred to homoploid hybrid speciation as a punctuated mode of speciation, in which long periods of hybrid zone stasis are followed by abrupt transitions in which a new fit hybrid genotype becomes established.

Hybridization and the Evolutionary History of Sunflowers

The role of hybridization in the diversification of North American sunflowers (*Helianthus* L.) was initially explored by Charles Heiser and his students (Heiser, 1947, 1949, 1951a, b; Heiser et al., 1969). Heiser documented the occurrence of natural hybrids between the widespread, common sunflower, *H. annuus* L., and several of its congeners, including *H. argophyllus* Torr. & A. Gray (Heiser, 1951a), *H. bolanderi* A. Gray (Heiser, 1949), *H. debilis* Nutt. (Heiser, 1951b), and *H. petiolaris* Nutt. (Heiser, 1947). This hybridization, Heiser argued, allowed *H. annuus* to acquire favorable alleles from the locally adapted species, thereby increasing its ecological amplitude and facilitating range expansion. In some instances, hybridization was believed to have contributed to the formation of introgressive races (*H. annuus* subsp. *texanus* Heiser in Texas (Heiser, 1951b) and *H. bolanderi* subsp. *bolanderi* in California (Heiser, 1949)) or new species (*H. neglectus* Heiser (Heiser et al., 1969)).

My laboratory re-examined these hypotheses using a combination of molecular marker surveys and molecular phylogenetic analyses (Dorado et al., 1992; Rieseberg et al., 1988, 1990a, b, 1991a, b; Rieseberg, 1991). We verified much of Heiser's work, including the occurrence of natural hybridization between *Helianthus annuus* and each of the species listed above (Dorado et al., 1992; Rieseberg et al., 1988, 1990a, b, 1998), as well as the introgressive origin of *H. annuus* subsp. *texanus* (Rieseberg et al., 1990b). On the other hand, the molecular evidence failed to support a hybrid origin for *H. neglectus* or *H. bolanderi* subsp. *bolanderi* (Rieseberg et al., 1988). Thus, while the morphological criteria employed by Heiser accurately identified contemporary hybrid swarms or zones, their utility in the detection of ancient, stabilized hybrid lineages was limited. This was not unexpected, as it has long been recognized that morphological intermediacy may sometimes result from processes other than hybridization (Gottlieb, 1972).

In addition to verifying or refuting putative examples of hybrid lineage formation, molecular phylogenetic analyses detected unsuspected hybrid origins of three species (Fig. 1): *Helianthus anomalus* Blake, *H. deserticola* Heiser, and *H. paradoxus* Heiser (Rieseberg et al., 1990b, 1991a; Rieseberg, 1991). The three hybrids appear to be derived from the same parental species, *H. annuus* and *H. petiolaris*. However, there are subtle differences in the parental chloroplast and nuclear ribosomal DNA haplotypes found in each hybrid, suggesting that each was independently derived (Rieseberg, 1991; Rieseberg et al., 1991a). Over the past decade we have exploited this replicated, natural hybrid speciation experiment, in combination with theoretical studies, to derive a more predictive theory of hybrid speciation. This body of work is described below.

Natural History

The three hybrid species and their parents are self-incompatible, insect-pollinated annuals, with the same chromosome number ($n = 17$). All five species are native to the continental United States. The two parental species have widespread and broadly overlapping distributions that are centered in the U.S. Great Plains (Fig. 2). They differ in soil preferences,

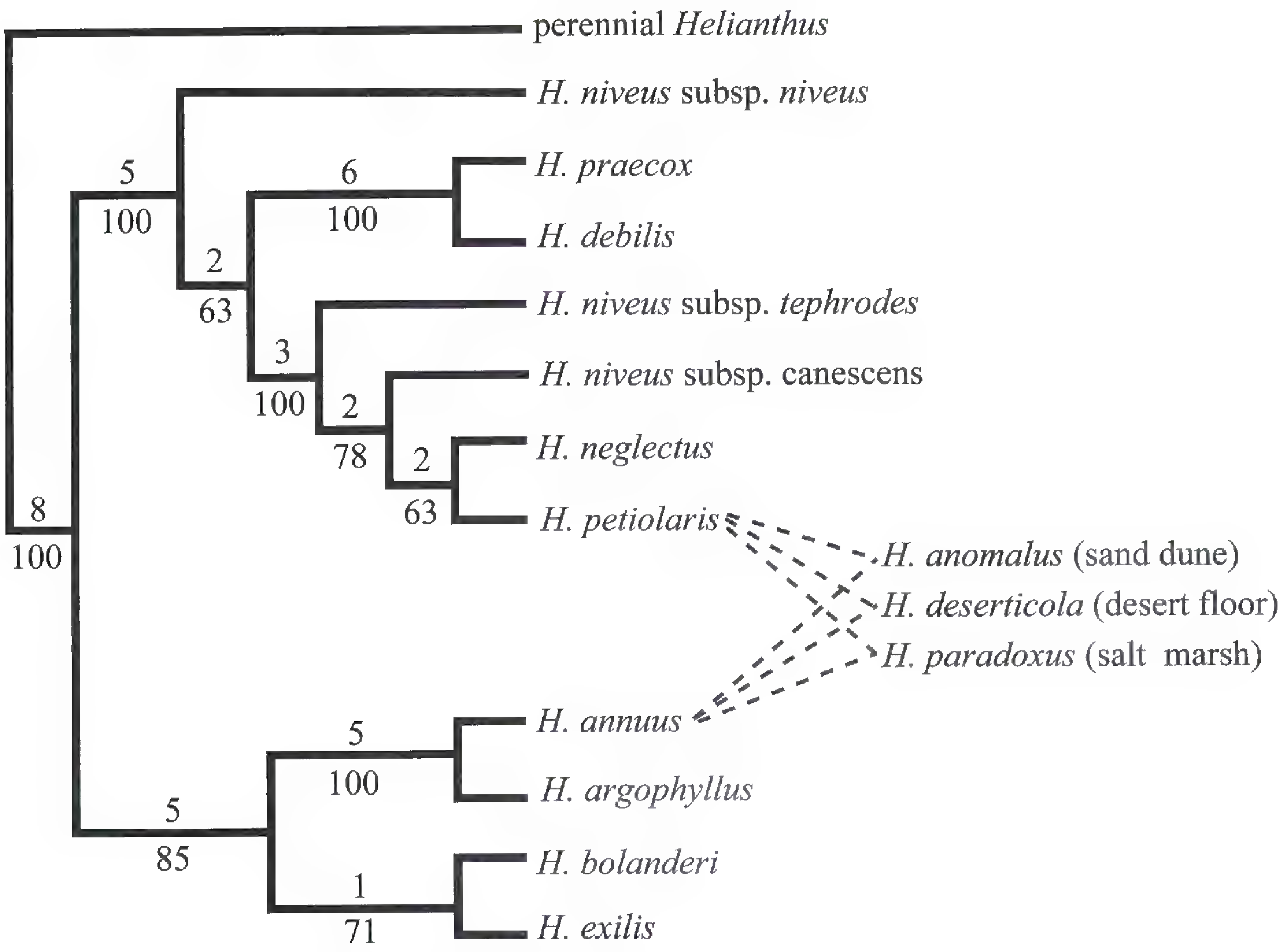

Figure 1. Phylogenetic tree for *Helianthus* sect. *Helianthus* based on combined chloroplast DNA and nuclear ribosomal DNA data (redrawn from Rieseberg, 1991, fig. 9). The number of mutations are given above and bootstrap percentages below each branch. Dashed lines indicate parentage of homoploid hybrid species.

however, with *Helianthus annuus* largely restricted to heavy, clay soils, and *H. petiolaris* to dry, sandy soils (Fig. 3). Nonetheless, these two habitats are often found in close proximity in the central and western United States, resulting in the production of numerous hybrid swarms and hybrid zones. The hybrid zones are narrow, often less than 30 m, and little evidence of introgression is found outside of the hybrid zones, apparently due to the synergistic action of several reproductive barriers (Rieseberg et al., 1995a, 1999b; Schwarzbach et al., 2001).

The three hybrid species are much more limited in geographic distribution than their parents (Fig. 2), with restriction of *Helianthus deserticola* to the Great Basin Desert in Nevada, Utah, and northern Arizona, *H. anomalus* to a handful of sand dune habitats in Utah and northern Arizona, and *H. paradoxus* to saline wetlands in western Texas and New Mexico (Fig. 3). Despite proximity to parental populations, no natural hybrids have been reported between the three ancient hybrid species and their parents. In contrast, the three hybrid species are almost completely allopatric to each other, but I have observed hybrids between *H. anomalus* and *H. deserticola* at the only site where they co-occur, Little Sahara Recreation Area in Central Utah.

Wild sunflower species produce an indehiscent one-seeded fruit called an achene (or cypsela). Although the achenes are eaten by small mammals and birds, dispersal by way of the animal feces seems unlikely because most seeds are likely to be digested. It seems more likely that sunflowers are dispersed by large mammals such as bison. Wild sunflower achenes are covered with small hairs that can bind to fur, and sunflower achenes have been reported in buffalo fur (Asch, 1993). There also are reports from early settlers of an association between bison and sunflowers. For example, in 1839 journalist Matthew Field described how "among the sunflower beds the huge back of a buffalo here and there was seen, as the ponderous brute broke down the stalks before him while pressing toward a fresher pasture ground" (cited in Asch, 1993: 12).

In addition to their role in dispersal, the disturbance generated by bison may have created opportunities for hybridization. Hybridization has long been known to be associated with natural and anthropogenic disturbance (Anderson, 1948), and, as shown by

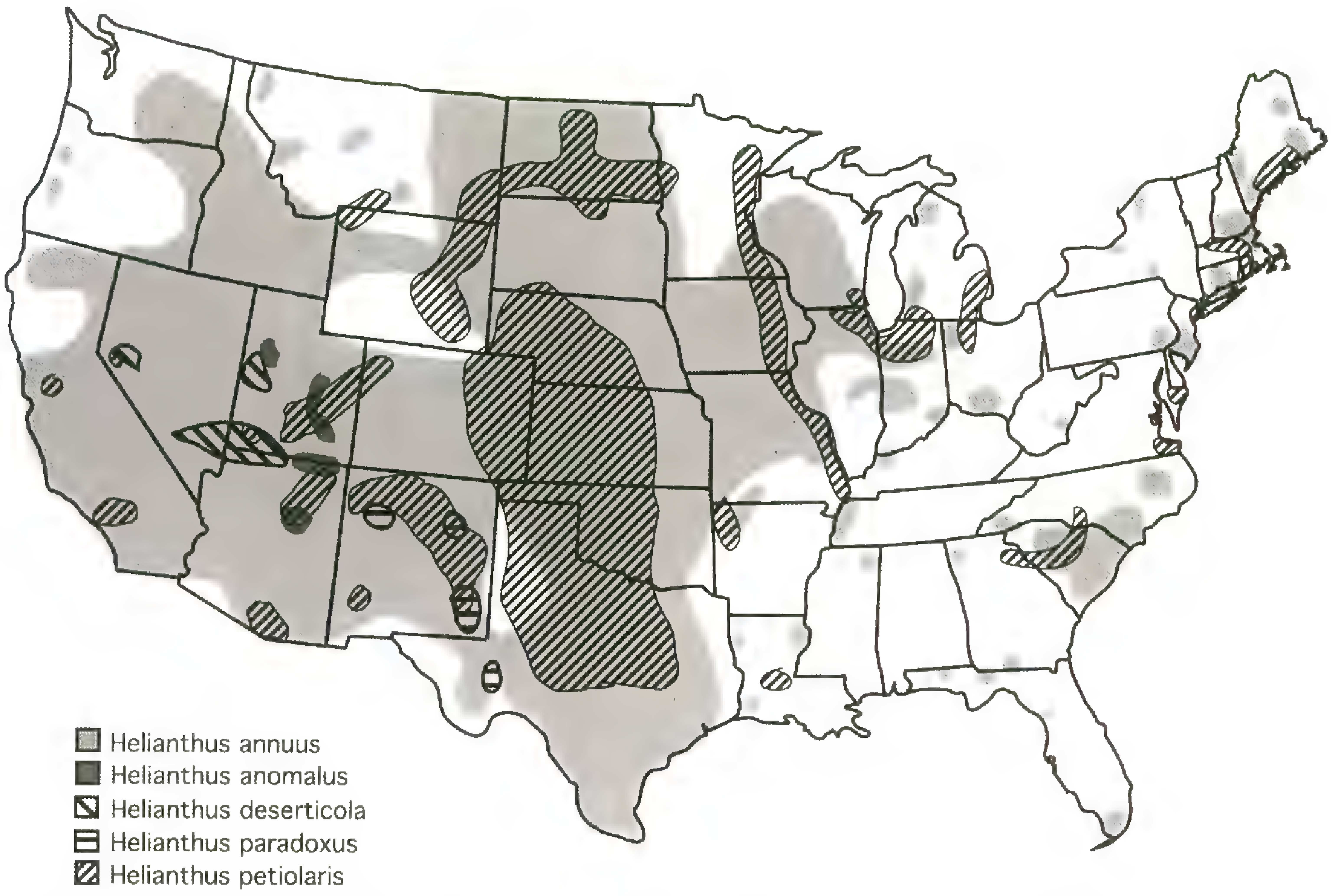

Figure 2. Geographic distributions of the two parental species and their three hybrid derivative species.

the following passage from Barsness (1985: 1), the impact of bison on the Great Plains was profound: "The [bison] herds marked their territory with trails, thousands of them, some shallow traces, some eight-to-ten-inch trenches, others so deep that the animal's sides would rub the embankments." Reflecting either cause or coincidence, microsatellite divergence places the origin of the three hybrid *Helianthus* species between 63,000 and 210,000 generations ago (Schwarzbach & Rieseberg, 2002; Welch & Rieseberg, 2002b; Gross et al., 2003), or just after the colonization of North America by bison ca. 200,000 years ago (Dary, 1974).

Karyotypic Evolution

As discussed earlier, theory indicates that the development of reproductive isolation between the new hybrid lineages and their parental species may be facilitated by rapid karyotypic evolution (Grant, 1981; McCarthy et al., 1995; Buerkle et al., 2000, 2003). Most verbal and simulation models have assumed that the karyotypic change occurs through the sorting of preexisting chromosomal rearrangements that differentiate the parental species (Stebbins, 1957; Grant, 1958). However, Templeton (1981) noted that recombination in hybrids might lead to additional chromosomal breakage.

To assess the role of genomic restructuring in hybrid speciation, we have generated detailed genetic linkage maps for the three hybrid species, *Helianthus anomalus*, *H. deserticola*, and *H. paradoxus*, as well as their putative parental species, *H. annuus* and *H. petiolaris* (Rieseberg et al., 1993, 1995b; Ungerer et al., 1998; Burke et al., 2002; Rieseberg et al., 2003). These maps were developed using a combination of AFLP, RAPD, and SSR (microsatellite) markers, with more than 650 markers placed on each map. Alignment of orthologous markers across the five maps allowed us to reconstruct the chromosomal rearrangements that have accompanied hybrid speciation.

All three hybrids have undergone massive karyotypic re-organization. Not only does each of the hybrid species possess a unique combination of parental chromosomal rearrangements, but also a minimum of three, two, and five chromosomal breakages (and an equal number of fusions) are required to achieve the *Helianthus anomalus*, *H. deserticola*, and *H. paradoxus* genomes, respectively (Rieseberg et al., 1995b, 2003; Burke et al., 2004; Lai et al., 2005). We have previously shown that approximately 50% of the reproductive barrier between *Helianthus* species is caused by chromosomal rearrangements (Rieseberg et al., 1999b). Furthermore, crossability and interfertility studies (Rieseberg, 2000, unpublished) indicate the

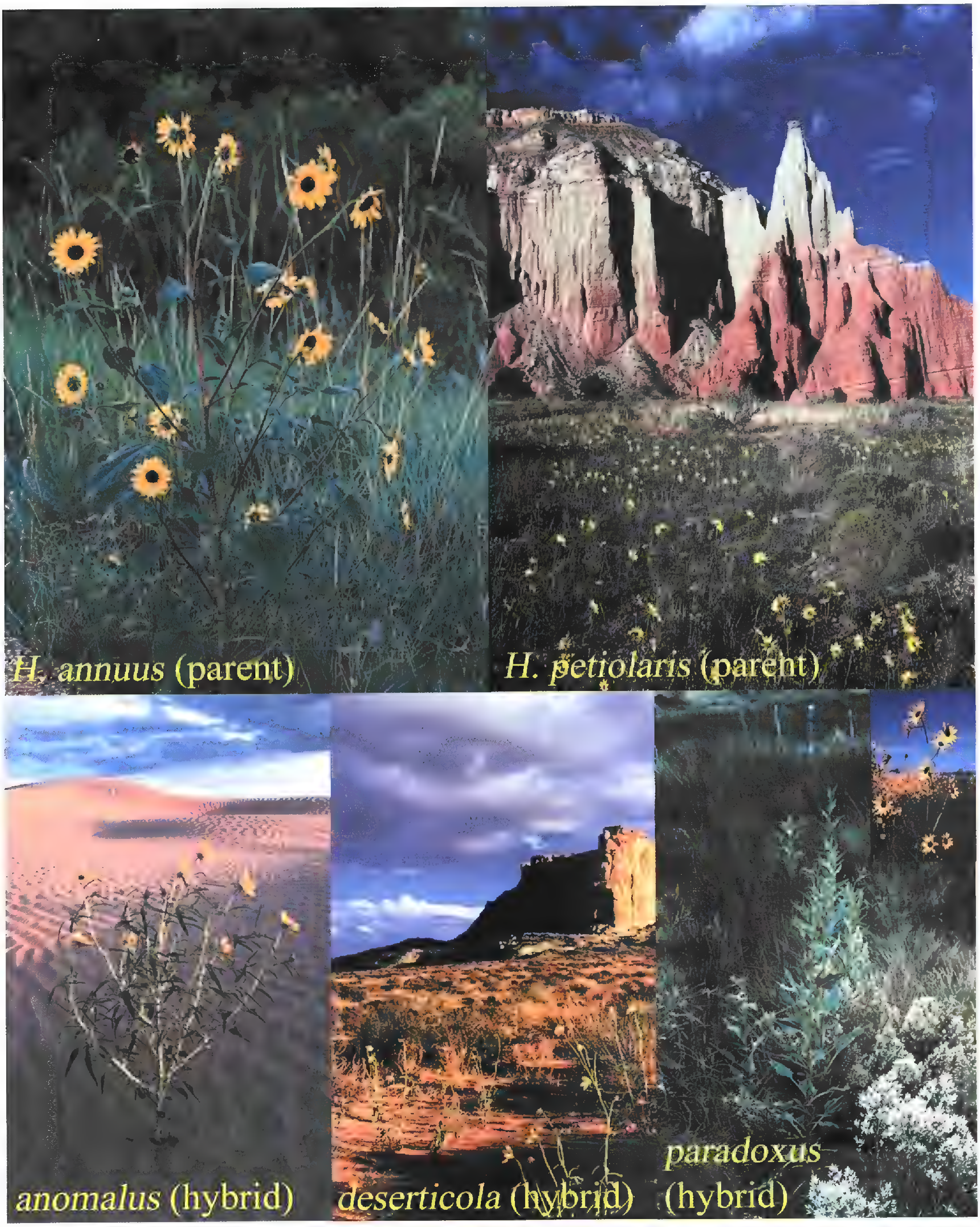

Figure 3. Photographs of the two parental species and their three hybrid derivative species in typical habitats. Photographs by Jason Rick.

three hybrid species are strongly isolated from each other and from their parental species (Fig. 4). Thus, as predicted by theory, rapid karyotypic evolution in the hybrid sunflower species appears to have facilitated the development of reproductive isolation with their parental species (Templeton, 1981; Buerkle et al., 2000).

Experimental Syntheses of Homoploid Hybrid Species

There is a rich literature describing the recovery of fertility in synthetic hybrid lineages and the degree of their isolation from their parental species (Stebbins, 1957; Grant, 1966a, b, 1981). These early studies were important because they demonstrated that

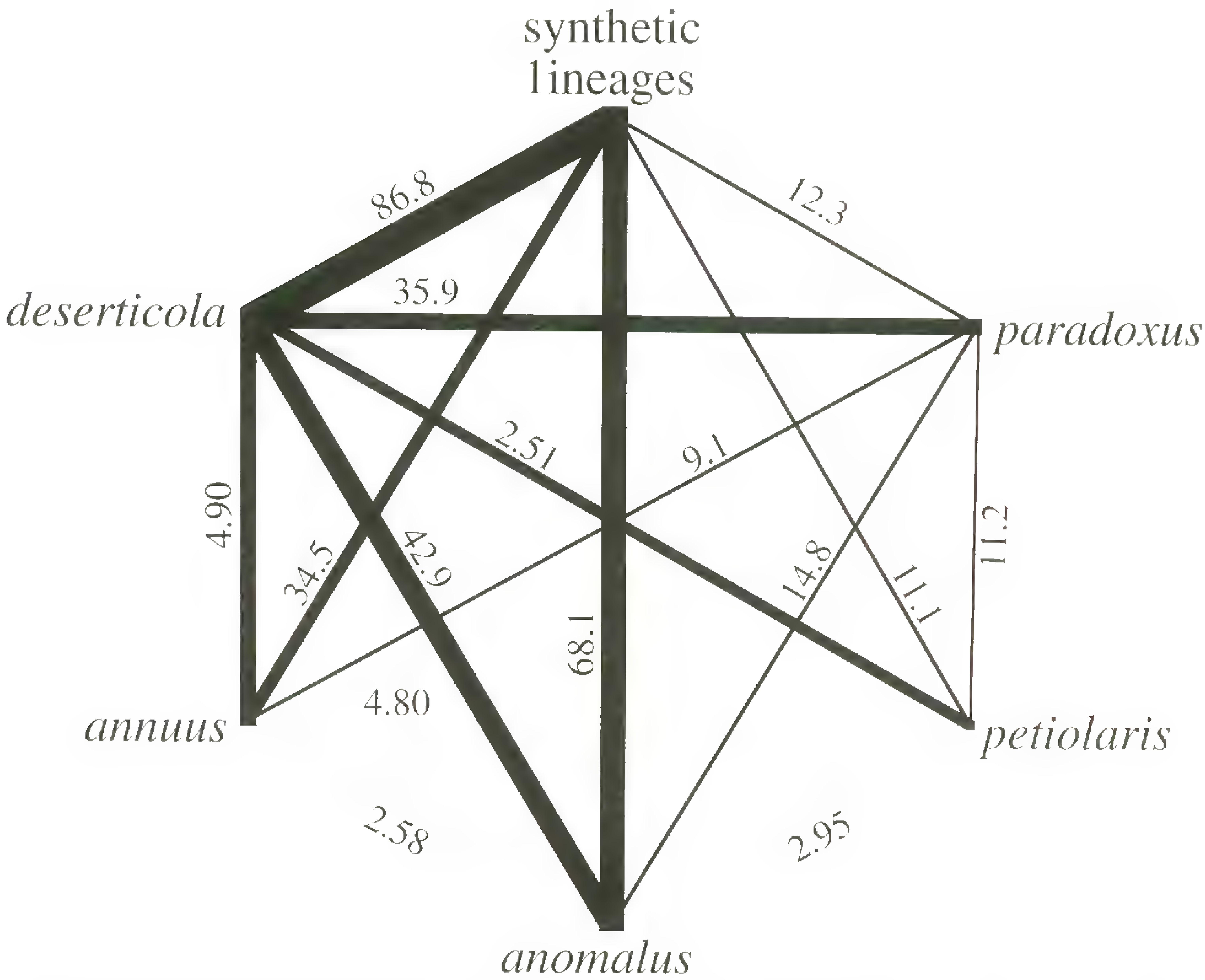

Figure 4. Crossability and interfertility among the two parental species, synthetic hybrid lineages, and three hybrid derivative species. Percentages indicate pollen viability of first generation hybrids. Line thickness is proportional to reproductive compatibility.

homoploid hybrid speciation was feasible. However, they did not attempt to replicate naturally occurring hybrid species or compare the newly synthesized hybrid lineages with those already existing in nature. The *Helianthus* work fills this important gap in the literature.

We attempted to replicate the origins of the hybrid species by synthesizing hybrids between the two parental species, *Helianthus annuus* and *H. petiolaris*, and subjecting the synthetic hybrids to selection for fertility over several generations (Rieseberg et al., 1996). Because sunflowers are self-incompatible and early generation hybrids are semi-sterile, hybrid speciation in this group likely involved both backcrosses and filial crosses. Therefore, we employed both kinds of crosses, but varied the order of backcross and filial generations in three independent experiments.

The results were gratifying. After only four generations of selection, pollen fertility in the three hybrid lineages had increased from 5.6 to 91.8%, indicating that the recovery of fertility not only was feasible, but that it potentially could occur very rapidly (Ungerer et al., 1998). In addition, the synthetic hybrid lineages were strongly isolated from their parental species, with mean pollen fertility ranging from 29 to 42% for crosses with *Helianthus annuus* and 10 to 13% for crosses with *H. petiolaris* (Fig. 4; Rieseberg, 2000). Remarkably, the three independently generated hybrid lineages were highly interfertile when crossed with each other; mean pollen fertility ranging from 83 to 89% (Rieseberg, 2000). This result implies that the three hybrid lineages have converged onto a fairly similar set of parental genes or chromosomal segments. Indeed, meiotic analyses indicated the synthetic lineages were similar in karyotype, varying in only one or two reciprocal translocations (Rieseberg, 2000).

To explore the genomic similarity of the synthetic hybrid lineages, we screened ca. 60 individuals from each lineage with 197 molecular markers specific to one or the other parental species (Rieseberg et al., 1996). Genomic congruence, as measured by the ϕ coefficient (a standard measure of association that can

vary from −1 to 1; Sokal & Rohlf, 1995), ranged from 0.65 to 0.75 ($P < 0.0001$) for comparisons among the three hybrid lineages, a result that accords well with the high fertility reported for crosses between these lineages (Rieseberg, 2000).

Given the congruence in genomic composition among the synthetic hybrid lineages, it seemed sensible to determine if the three natural hybrid species had found a similar solution to the problem of hybrid sterility. This was a more difficult problem that required surveying natural populations of both *Helianthus annuus* and *H. petiolaris* to determine the likely parental origin of each marker mapped in the three hybrid species (Rieseberg et al., 1993, 1995b, 2003; Ungerer et al., 1998). In all, 427, 290, and 325 of the markers mapped in *H. anomalus*, *H. deserticola*, and *H. paradoxus*, respectively, could be assigned to one or the other parental species and thus were informative with respect to genomic composition (Rieseberg et al., 2003). Genomic congruence was high for comparisons between the three synthetic hybrid lineages and either *H. anomalus* or *H. deserticola*: ϕ ranged from 0.44 to 0.50 ($P < 0.0001$) for comparisons with *H. anomalus* (Rieseberg, 2000) and 0.53 to 0.59 ($P < 0.0001$) for comparisons with *H. deserticola* (Rieseberg, unpublished). In contrast, little congruence was observed between the three synthetic lineages and *H. paradoxus*: 0.28 to 0.34 ($P < 0.01$). Also, note that levels of genomic congruence accord closely with crossing relationships (Fig. 4); the synthetic hybrids are most compatible and most interfertile with *H. anomalus* and *H. deserticola* as predicted by genomic congruence, but least compatible and least interfertile with *H. paradoxus*. From a broader perspective, these results indicate that fertility selection plays a major role in determining hybrid genomic composition and that the number of solutions to the problem of hybrid sterility may be fairly limited. Clearly, *H. paradoxus* has found a different solution than the other taxa. Possibly, there were different proportions of the parental species in the hybrid zone from which *H. paradoxus* was founded and/or the genomic composition of *H. paradoxus* was strongly influenced by ecological selection (Lexer et al., 2003a, b; Rieseberg et al., 2003).

Tempo of Hybrid Speciation

Both theoretical and experimental studies of homoploid hybrid speciation indicate that it is likely to occur very rapidly (Stebbins, 1957; Grant, 1966a, b; Rieseberg et al., 1996; McCarthy et al., 1995; Buerkle et al., 2000), but until recently no methods have been available to test this prediction. We have devised a method for estimating the tempo of hybrid speciation in nature (Ungerer et al., 1998). The rationale for our method is that in a newly forming hybrid species the sizes of parental chromosomal segments are expected to become progressively smaller over time due to recombination (Fisher, 1953; Baird, 1995). However, continued reduction in segment size will be countered by stabilization of the hybrid species' genome; subsequent recombination will be among segments derived from the same parental species (Ungerer et al., 1998). This analysis represents an empirical application of R. A. Fisher's junctions approach (Fisher, 1953), which tracks parental species segments by monitoring recombination breakpoints or "junctions" between heterogeneous regions rather than all points on a genome. In a neutral case, we can imagine a "junctions clock," which is analogous to the molecular clock, but slows over time as heterozygosity decreases due to drift. By comparing the frequency spectrum of observed parental species' chromosomal segments with predictions based on computer simulations (Ungerer et al., 1998), it is possible to estimate the number of generations required to stabilize the genome of a hybrid species. Note that we are estimating the speed of hybrid speciation, not the age of the hybrid species.

To date, we have only estimated the tempo of speciation for one of the hybrid species, *Helianthus anomalus* (Ungerer et al., 1998). This species has the largest number of mapped species-specific markers, thereby allowing the most precise empirical estimates of chromosomal segment lengths (Ungerer et al., 1998). It seems likely that the hybrid species will arise in hybrid founder populations that are spatially and/or ecologically isolated from the parental species. Therefore, we modeled this scenario by simulating a hybrid swarm, starting with equal numbers of *H. annuus* and *H. petiolaris* individuals, and allowing recombination to take its course in small, closed populations of different sizes and under different selection regimes. The speed of hybrid speciation was estimated by comparing the sizes of chromosomal segments in the simulation studies with those of *H. anomalus*. Chromosomal segment sizes in the *H. anomalus* genome were large, suggesting that its genome became stabilized in 10 to 60 generations. This result accords well with earlier simulation studies of hybrid speciation in which new hybrid species typically became established in ca. 50 generations (McCarthy et al., 1995; Buerkle et al., 2000) and argues that the tempo of homoploid hybrid speciation, like allopolyploidy, is very rapid.

Phenotypic Divergence

The three hybrid species inhabit what are arguably the most extreme habits of any sunflower (dune, desert

Table 1. Hypothetical example of transgressive segregation due to the complementary action of genes with additive effects (from Rieseberg et al., 2003).

	Phenotypic values			
QTLs	Species A (AA genotype)	Species B (BB genotype)	Transgressive F_2	Transgressive F_2
1	+1	−1	+1(AA)	−1(BB)
2	+1	−1	+1(AA)	−1(BB)
3	+1	−1	+1(AA)	−1(BB)
4	−1	+1	+1(BB)	−1(AA)
5	−1	+1	+1(BB)	−1(AA)
Total	+1	−1	+5	−5

floor, and salt marsh habitats; Fig. 3) and have diverged significantly from the parental species for many traits associated with these habitats (Schwarzbach et al., 2001; Rosenthal et al., 2002). An important question is whether hybridization could provide the phenotypic variation necessary for colonization of these habitats.

We addressed this question by comparing phenotypic variation in the three ancient hybrid species, synthetic hybrids (a BC_2 population of *Helianthus annuus* × *H. petiolaris*), and both parental species grown in a common greenhouse environment (Rosenthal et al., 2002; Rieseberg et al., 2003). A total of 40 morphological, life history, and ecophysiological traits were measured.

As expected, given their divergent habitat preferences, the ancient hybrid species differed significantly from the parental species for many of the measured traits: 20 for *Helianthus anomalus* (8 intermediate, 12 extreme), 14 for *H. deserticola* (4 intermediate, 10 extreme), and 24 for *H. paradoxus* (8 intermediate, 16 extreme). Intermediate traits are easily accounted for by hybridization because the entire phenotypic continuum between the parental species is found in segregating hybrids (Rieseberg et al., 2003).

Hybridization could account for most of the extreme traits as well. Indeed, for 28 of the 40 traits, BC_2 plants had phenotypic values that significantly exceeded those of the parental species, a phenomenon known as transgressive segregation (Grant, 1975). Overall, 10 of 12 (83.3%), 10 of 10 (100%), and 11 of 16 (68.8%) extreme traits in *Helianthus anomalus*, *H. deserticola*, and *H. paradoxus*, respectively, were within the range of the BC_2 population. The handful of trait values exceeding those in the BC_2 population might have been transgressive in a reciprocal backcross population or have arisen through mutational divergence rather than hybridization. In either case, it is clear that the majority of extreme traits observed in the ancient hybrid species could have been generated through hybridization. These results have now been replicated by similar common garden experiments conducted in the natural habitats of each of the parental species (Lexer et al., 2003a; Gross et al., 2004; Ludwig et al., 2004). Thus, transgressive segregation, which is commonly observed in segregating hybrid populations (Rieseberg et al., 1999a), provides a simple mechanism for the ecological divergence of hybrid lineages.

Genetics of Transgressive Segregation

So how are extreme phenotypes generated in hybrid populations? Numerous possibilities have been suggested (deVicente & Tanksley, 1993; Rieseberg et al., 1999a), including an elevated mutation rate, reduced developmental stability, non-additive effects of alleles at the same (overdominance) or different (epistasis) loci, unmasking of rare recessive alleles, and the combination of alleles with effects in the same direction from both parental species (complementary gene action; Table 1).

We employed quantitative trait locus (QTL) methods to determine the mode of gene action underlying transgressive segregation in *Helianthus* (Rieseberg et al., 2003). Briefly, the same BC_2 population employed for phenotyping in the previous section was genotyped for 96 molecular markers, and 185 QTLs were detected for the 40 traits. Remarkably, 39% of the QTLs had effects in the opposite direction of species differences and 34 of 40 traits had at least one opposing QTL. That is, for these QTLs, the *H. annuus* allele produced a more *H. petiolaris*-like phenotype, whereas the *H. petiolaris* allele produced a phenotype that was in the direction of *H. annuus*. This is exactly the kind of genetic architecture that is conducive for transgressive segregation under the complementary gene action model. Hybrid individuals that combine all of the "plus" or all of the "minus" QTLs from both parents for a given trait will have transgressive phenotypes (Table 1). Although complementary gene action explained most of the transgressive phenotypes, epistatic interactions were detected for 18 traits as well. These results are

similar to those obtained for cultivated plants; complementary gene action is most frequent, but epistasis and overdominance do sometimes contribute (deVicente & Tanksley, 1993; Rieseberg et al., 1999a).

Genetic Correlations

Transgressive segregation via complementary gene action provides a means by which extreme phenotypes may be generated for individual traits. For a hybrid lineage to successfully colonize a new habitat, however, all of the trait differences must be combined into a single individual or genotype, which may be difficult because of linkage and/or pleiotropy for QTLs underlying key traits. Thus, genetic correlations may limit ecological divergence through hybridization.

To determine the role of genetic correlations in the ecological divergence of the hybrid sunflower species, we asked whether closely linked or pleiotropic QTLs in the BC_2 population described above have effects that are in the same direction with respect to the hybrid species phenotype (Rieseberg et al., 2003). These positive correlations would greatly facilitate ecological divergence and hybrid speciation.

We found closely linked QTLs were indeed positively correlated in direction of effect (Rieseberg et al., 2003: Fig. 1). The ϕ coefficient of association ranged from 0.32 ($N = 256$; $P < 0.001$) for *Helianthus paradoxus*, to 0.47 ($N = 256$; $P < 0.001$) for *H. anomalus*, to 0.53 ($N = 256$; $P < 0.001$) for *H. deserticola*. Thus genetic correlations likely facilitated rather than impeded the origins of the three species, particularly for *H. anomalus* and *H. deserticola*. However, our results also imply that genetic correlations may limit the number of ecologically relevant multi-trait phenotypes, perhaps explaining why only three new hybrid species have originated from this cross.

Hybrid Species' Genomic Composition and Predicted Phenotypes

Although studies of synthetic hybrids demonstrate that most of the phenotypic differences associated with each of the hybrid species could have arisen through hybridization, they fail to prove that this is what actually happened. It could be, for example, that the differences arose as a consequence of mutational divergence and that hybridization was incidental to phenotypic evolution. To distinguish between these two hypotheses, we compared the genomic composition of the three ancient hybrid species with predictions from the QTL analyses of the BC_2 population of *Helianthus annuus* × *H. petiolaris* (Rieseberg et al., 2003). That is, we asked whether the hybrid species had the predicted set of QTL alleles for producing their phenotypes. If hybridization played a key role in phenotypic divergence, then a significant correlation should be found between predicted and actual genomic composition.

Genomic composition of the ancient hybrid species did accord closely with predictions from the QTL analyses (Rieseberg et al., 2003: Fig. 2). The ϕ coefficient of association ranges from 0.56 ($N = 150$; $P < 0.001$) for *Helianthus paradoxus*, to 0.58 ($N = 193$; $P < 0.001$) for *H. anomalus*, to 0.65 ($N = 94$; $P < 0.001$) for *H. deserticola* (Rieseberg et al., 2003). Thus, hybridization does appear to be largely responsible for the phenotypic divergence of the three hybrid species.

Earlier in this paper, I reviewed evidence suggesting that fertility selection plays a major role in shaping hybrid genomic composition (Rieseberg et al., 1996), whereas the QTL comparisons described above suggest that phenotypic (presumably ecological) selection must be important as well (Rieseberg et al., 2003). What is the relative importance of these two modes of selection? A preliminary comparison of the two data sets indicates that in many instances there is concordance between the predicted genomic composition from fertility selection and the QTL analysis of phenotypic differences, perhaps implying overlap between hybrid incompatibility genes and those responsible for phenotypic differences. Also, the combined data set more completely accounts for hybrid genomic composition than either individual data set does alone (Rieseberg, unpublished).

Phylogeography

Comparisons of the genomic composition of the ancient hybrid species with synthetic hybrid lineages and predictions from QTL studies (above) suggest that homoploid hybrid speciation may be repeatable. Thus, we asked whether the ancient hybrid species had arisen multiple times in nature. This was accomplished by surveying natural populations of the parental species and their three hybrid derivatives for variation at chloroplast DNA and nuclear microsatellite loci (Schwarzbach & Rieseberg, 2002; Welch & Rieseberg, 2002b; Gross et al., 2003). We also assessed crossability and interfertility among populations of *Helianthus anomalus* and *H. deserticola*. In *H. anomalus*, the crossing studies were complemented by meiotic analyses of inter-populational hybrids to determine the chromosomal basis of variation in fertility.

For a single origin, all populations of a given hybrid species are expected to have the same chloroplast

DNA haplotype, to form a monophyletic lineage based on nuclear microsatellite loci, and to be highly interfertile (i.e., have a single karyotype) when crossed. For multiple origins, different populations of a species may vary in chloroplast DNA haplotype and the species is unlikely to be monophyletic with respect to nuclear microsatellite loci. Also, significant variation in fertility due to karyotypic variability is predicted for inter-populational crosses. Note that multiple chloroplast DNA haplotypes and polyphyly for nuclear microsatellite loci can also result from a single origin followed by introgression with one or both parental species. However, substantial variation in inter-populational crossability and interfertility or karyotype is unlikely in this latter scenario (Schwarzbach & Rieseberg, 2002).

Molecular and crossability/interfertility evidence suggest at least three different origins for *Helianthus anomalus* (Schwarzbach & Rieseberg, 2002). The species has three main chloroplast DNA haplotypes, one apparently derived from *H. annuus* and the other two from *H. petiolaris*. Likewise, the species has three fertility groups that are completely correlated with the distribution of chloroplast DNA haplotypes. Meiotic analyses indicate the fertility groups differ by one or two reciprocal translocations, as would be predicted for multiple origins. However, there was no apparent signature of multiple origins in the nuclear microsatellite data, perhaps due to gene flow among the independently derived lineages subsequent to hybrid speciation.

Patterns of molecular variation in *Helianthus deserticola* were also most consistent with multiple origins (Gross et al., 2003). The species displayed four different chloroplast DNA haplotypes (one from *H. annuus* and three from *H. petiolaris*), polyphyly at microsatellite loci, and considerable inter-populational crossability and interfertility. There was little congruence between the three data sets, however, making it more difficult to rule out the possibility of a single hybrid speciation event followed by introgression with populations of the parental species.

In contrast to *Helianthus anomalus* and *H. deserticola*, *H. paradoxus* is derived from a single hybrid speciation event (Welch & Rieseberg, 2002b). All surveyed populations of the species share a single chloroplast DNA haplotype (derived from *H. annuus*) and form a single clade with 99.8% bootstrap support based on 17 microsatellite loci.

The apparent numbers of origins of the three hybrid species correlates well with the results from the morphological and QTL analyses. Ten of 12 extreme traits in *Helianthus anomalus* and all 10 extreme traits in *H. deserticola* could be re-created by hybridizing populations of the parental species. However, only 11 of 16 extreme traits in *H. paradoxus* could be replicated in synthetic hybrids, implying that the creation of the *H. paradoxus* phenotype may be a rare event. A similar pattern was observed for genetic correlations. Tightly linked QTLs mostly had effects in the same direction with respect to the phenotypes of the apparently multiply derived *H. anomalus* (ϕ = 0.47) and *H. deserticola* (ϕ = 0.53). In contrast, genetic correlations make it difficult to re-create the multi-trait phenotype of *H. paradoxus* (ϕ = 0.32), which appears to have arisen only once.

Ecological Selection

Theoretical studies indicate that strong ecological selection is a prerequisite for successful hybrid speciation (McCarthy et al., 1995; Buerkle et al., 2000). Also, our studies of phenotypic differentiation have assumed that ecological selection is the underlying force driving divergence. However, it may be that some of the phenotypic differences result from neutral processes or are a byproduct of selection on correlated traits. Correlated selection is likely to be particularly important in hybrid speciation, because the unit of selection is the chromosomal segment rather than individual gene or mutation.

We have employed both comparative and experimental approaches to identify traits likely to have been under selection during hybrid speciation. The comparative approach focuses on traits in the hybrid species that are common to other taxa sharing its habitat. For example, the sand dune endemic, *Helianthus anomalus*, has many traits associated with dune habitats such as very large, cylindrical seeds, rapid early root growth, and succulent leaves (Schwarzbach et al., 2001; Rosenthal et al., 2002). Large seeds are thought to represent an adaptation for burial avoidance, whereas a round or cylindrical shape may prevent seeds from being blown away from the dune habitat. Large seeds also likely contribute to rapid early root growth, which enables seedlings to tap into water reserves deeper in the sand dunes. Finally, succulent leaves may serve to reduce water loss and abrasion by blowing sand (Danin, 1991; Bowers, 1996). *Helianthus deserticola* has many of the classic features of a desert annual, including rapid flowering, reduced height at maturity, and small, narrow leaves (Rosenthal et al., 2002). The first two traits ensure rapid reproduction following heavy seasonal rain, whereas small narrow leaves decrease water loss and avoid fatal overheating (Chapin et al., 1987; Gibson, 1998). *Helianthus paradoxus* shares several traits with other salt-loving or halophytic species, including increased leaf succulence and an efficient mechanism for reducing mineral ion uptake (Welch & Rieseberg,

2002a; Lexer et al., 2003b). Both reduce the toxic effects of sodium and other mineral ions.

Our experimental studies involved the transplantation of reciprocal BC_2 synthetic hybrids into the habitats of the three ancient hybrid species. We then measured the strength of selection on individual traits and (for *Helianthus paradoxus*) the QTLs underlying them. For *H. anomalus*, we focused on leaf ecophysiological traits, phenology, and vegetative biomass, with fitness estimated as reproductive biomass (Ludwig et al., 2004). Although we had predicted that selection in the synthetic hybrids would mostly be in the direction of the *H. anomalus* phenotype, this was not necessarily the case. Only for leaf succulence in the BC_2ann hybrids (backcrosses toward *H. annuus*) and water use efficiency in the BC_2pet hybrids (backcrosses toward *H. petiolaris*) was selection toward the *H. anomalus* phenotype. For most traits, the direction of selection was dependent on the genetic background, suggesting the existence of multiple adaptive peaks for *Helianthus* in the dune habitat. Although these results seem inconsistent with the multiple origins of the species (Schwarzbach & Rieseberg, 2002), it may be that fertility selection or selection on other correlated traits drive early generation hybrids toward just one of these peaks.

Results from the selection analyses in the *Helianthus deserticola* environment were equally difficult to interpret (Gross et al., 2004). For two of the key traits, leaf area and flowering date, selection differentials and gradients differed in sign in both of the BC_2 populations. Thus, while it is clearly feasible for directional selection to produce the *H. deserticola* phenotype for these traits, it is not possible to predict the phenotypic outcome of such selection from the present experiment. For the third key trait, stem diameter, selection in the synthetic hybrids was consistent, but in the opposite direction of the *H. deserticola* phenotype. This result is puzzling and may possibly relate to the experimental design, in which seedlings were propagated at Indiana University and then transported to Utah for transplantation. In such weak and etiolated seedlings, it may be that large stems would be favored, whereas narrow stems might be favored in seedlings propagated under natural, high light conditions.

Only in *Helianthus paradoxus* habitat was the direction of selection in the experimental hybrids consistently in the direction of the *H. paradoxus* phenotype (Lexer et al., 2003b). Positive directional selection was detected for leaf succulence and Ca uptake, two traits that are known to mitigate salt stress in plants. In contrast, the uptake of Na and other toxic mineral ions was strongly negatively selected in the salt marsh habitat. Of greater significance was the observation that QTLs underlying both mineral ion uptake traits and survivorship in the salt marsh had effects in opposing directions (Lexer et al., 2003a). As discussed earlier, this kind of genetic architecture underlies transgressive segregation and provides a simple explanation for how the salt marsh habitat of *H. paradoxus* might have been originally colonized by hybrids.

The QTL data also allowed us to test a fundamental requirement for homoploid hybrid speciation. Homoploid hybrid speciation represents a kind of sympatric or parapatric speciation, and models of speciation with gene flow indicate the strength of selection at individual loci must be greater than the migration rate (Maynard Smith, 1966). Therefore, we calculated selection coefficients for mineral ion QTLs in the salt marsh habitat (Lexer et al., 2003a). The selection coefficients were larger (-0.08 to $+0.13$) than any conceivable migration rate for sunflowers, indicating it would have been feasible for *Helianthus paradoxus* to arise in sympatry or parapatry with its parental species.

Candidate Genes for Ecological Divergence

Finally, we have assayed sequence polymorphisms for salt tolerance candidate genes in these same BC_2 populations to determine whether any of the candidate genes map to QTLs of interest, as well as to identify additional genomic regions associated with salt tolerance (Lexer et al., 2004). The salt tolerance candidates were identified from an expressed sequence tag (EST) library for *Helianthus paradoxus* based on homology to genes with known function. One of the 11 genes, a Ca-dependent protein kinase (CDPK), maps coincident with a previously identified QTL for mineral ion uptake. Two additional genes (an ER-type calcium ATPase and a transcriptional regulator) also exhibit a significant fitness effect in the wild. Of course, these studies are correlational only and function will have to be verified by transgenic complementation or RNAi. Nonetheless, they indicate we soon may be able to examine the role of individual genes in ecological divergence and speciation in sunflowers.

Conclusions and Future Directions

Over the past 15 years, my lab has studied how new hybrid species may arise without a change in chromosome number. Our main contributions include:

(1) Molecular documentation of the hybrid origin of three distinct sunflower species from the same pair of parental species (Rieseberg et al., 1990b; Rieseberg, 1991).

(2) Development of the first genetic map for a homoploid hybrid species (Rieseberg et al., 1993).
(3) Demonstration that homoploid hybrid speciation in wild sunflowers has been accompanied by rapid karyotypic evolution as predicted by verbal models (Rieseberg et al., 1995b; Lai et al., 2005).
(4) Experimental re-creation of homoploid hybrid species in sunflower and demonstration of genomic congruence of synthetic and ancient hybrid species (Rieseberg et al., 1996). This demonstrated the repeatability of homoploid hybrid speciation and the importance of fertility selection in shaping hybrid genomic composition.
(5) Demonstration of the rapid tempo of hybrid speciation based on the large sizes of parental chromosomal blocks in a hybrid sunflower species (Ungerer et al., 1998).
(6) Computer simulation of homoploid hybrid speciation, which verified verbal theory and demonstrated the evolutionary conditions favorable to hybrid origin differ from those required for the independent evolution of the hybrid species (Buerkle et al., 2000).
(7) Re-creation of phenotypes of homoploid hybrid species by experimental hybridization of contemporary parental species populations and transgressive segregation (Lexer et al., 2003b; Rieseberg et al., 2003; Gross et al., 2004; Rosenthal et al., 2005).
(8) Demonstration that complementary gene action is the primary cause of transgressive segregation in experimental sunflower hybrids (Lexer et al., 2003b; Rieseberg et al., 2003).
(9) Discovery that genetic correlations facilitate rather than impede the origin of the hybrid sunflower species (Rieseberg et al., 2003).
(10) Demonstration that the genomic composition of the ancient hybrid sunflower species can be predicted from the QTL analysis of phenotypic traits, implying an important role for ecological selection in shaping hybrid genomic composition (Rieseberg et al., 2003).
(11) Discovery that two of the hybrid sunflower species are multiply derived in nature as predicted from earlier studies of the repeatability of hybrid speciation (Schwarzbach & Rieseberg, 2002; Welch & Rieseberg, 2002b; Gross et al., 2003).
(12) Demonstration that many of the transgressive traits discovered in experimental crosses are under selection in natural hybrid habitats (Lexer et al., 2003a; Ludwig et al., 2004; Gross et al., 2004).
(13) Demonstration that selection coefficients for QTLs underlying ecological divergence in *Helianthus paradoxus* are large enough to account for the origin of the species in parapatry with its parental species (Lexer et al., 2003b).
(14) Identification of several promising candidate genes for ecological divergence in *Helianthus paradoxus* (Lexer et al., 2004).

Of course, there is much left to do. Previously, we attempted to replicate the early stages of hybrid speciation by planting segregating hybrids into the habitat of the ancient hybrid species and identifying traits and QTLs that were under selection. We are currently extending these experiments by asking whether we can detect the molecular signature of selection during hybrid speciation and if the same chromosomal segments that were under selection in the experimental populations were also under selection when the species arose in nature more than 63,000 years ago. Preliminary evidence suggests we can. Microsatellite markers flanking the three most strongly selected QTLs in the *Helianthus paradoxus* habitat had significantly reduced variability as compared with microsatellite loci from unselected regions, yet there was no difference in variability levels between these groups of loci in the parental species (C. Edelist et al., unpublished).

Second, my lab has developed a 3000-gene abiotic stress microarray for sunflower (Lai et al., in press). We wish to ask whether gene expression differences are induced by hybridization and whether these induced differences contribute to ecological divergence and hybrid speciation.

Third, we wish to use the hybrid species system to address the fundamental question of whether adaptive divergence within a species is limited by mutation or by gene flow from the center of each species range (Kirkpatrick & Barton, 1997). That is, why did the parental species not colonize the extreme habitats of the ancient hybrid species? Put another way, was it new hybrid gene combinations or reproductive isolation that allowed the hybrid species to colonize new habitats?

Finally, we will continue our work to identify and characterize the genes underlying ecological divergence in this system. This will involve a combination of EST sequencing (> 70,000 ESTs already sequenced), searches for genes with the signature of positive selection (> 30 identified), candidate gene mapping (close to 300 mapped), microarray analyses, and functional testing using transgenic complementation and RNAi.

Although this review has focused almost exclusively on hybrid sunflower species, there are broader issues that need to be addressed as well. In particular, we need to know how frequently homoploid hybrid speciation occurs in nature, which will require better tools for detecting it in phylogenetic trees. Fortunately, help is on the way. New methods of network reconstruction are under development (reviewed in Linder & Rieseberg, 2004), and the availability of sequence data from numerous nuclear genes should provide far more power for detecting reticulate histories than was possible in the past. This power could be further enhanced if clusters of linked genes were sequenced. Under the assumption of hybrid speciation, separate phylogenetic reconstructions of individual genes that are tightly linked should have the topology of only one side of the hybridization. These reconstructions would be topologically incongruent with reconstructions based upon clusters of genes from the other side of the hybridization.

We also need to know whether many of the discoveries made in the sunflower system can be generalized to other homoploid hybrid species. How

are most new hybrid species reproductively isolated from their parental species? Is ecological divergence the rule rather than the exception? Are the habitats of the new hybrid species typically extreme relative to their parental species, or are they more accurately described as intermediate or recombinant? What is the genetic basis of the ecological divergence in hybrids? How repeatable is hybrid speciation in other lineages? Are homoploid hybrid species often multiply derived? What are the characteristics of taxa that make them prone to homoploid hybrid speciation? Hopefully, our sunflower work will provide an experimental and conceptual guide for studies of homoploid hybrid species in other organismal groups.

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ADAPTIVE RADIATION AND EVOLUTION OF BREEDING SYSTEMS IN *SCHIEDEA* (CARYOPHYLLACEAE), AN ENDEMIC HAWAIIAN GENUS[1]

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Abstract

A multi-disciplinary approach, including phylogenetic analysis, population biology, and quantitative genetics, has helped to elucidate the selective factors that have promoted speciation and shifts in breeding systems in *Schiedea* (Caryophyllaceae). *Schiedea* is the fifth largest lineage in the native Hawaiian flora and the most diverse lineage with respect to breeding systems. The genus is monophyletic and shares a common ancestor with a clade consisting of two arctic or boreal-north temperate species. Most inter-island colonizations were from older to younger islands, and most movement between islands led to sufficient isolation to result in formation of new species that are single-island endemics rather than species with multi-island distributions. Closely related species pairs occurring on older islands tend to differ in habitat and are isolated ecologically on the same island, while species pairs on younger islands tend to be in similar habitat on different islands. Speciation within this lineage has been associated with shifts in habitat, pollination system, and breeding system, including evolution of selfing (obligate autogamy, facultative autogamy), mixed mating systems, and dimorphism (gynodioecy, subdioecy, and dioecy). Dimorphic breeding systems appear to have been derived independently twice in *Schiedea*, and facultative autogamy and obligate autogamy have both evolved three times. The colonization of windy, dry habitats appears to occur before changes in sex allocation patterns, and the evolution of dimorphism in this lineage has been promoted by the combination of high inbreeding depression and high selfing rates. Many morphological traits associated with allocation to male and female function are highly heritable, and genetic correlations in general do not appear to constrain the evolution of dimorphism in *Schiedea*.
Key words: adaptive radiation, autogamy, breeding systems, Hawaii, inbreeding depression, resource allocation, *Schiedea*, selfing, sexual dimorphism.

Flowering plants reproduce with a remarkable diversity of breeding systems, even among closely related species, and the selective forces responsible for this diversity continue to be of great interest. Adaptive radiations in island systems have been particularly useful because the isolation of remote archipelagos has made it easier to identify selective factors and to discern evolutionary patterns (e.g., Wagner & Funk, 1995; Givnish & Sytsma, 1997; Grant, 1998). The Hawaiian Islands have been of particular interest in the study of plant mating systems because of the high incidence of dioecy in the flora. Worldwide, the average incidence of dioecy in angiosperm floras is about 4%–6% (Renner & Ricklefs, 1995), but the Hawaiian Islands have the highest incidence of dioecy of any angiosperm flora studied (14.7%), followed closely by the New Zealand flora (12%–13%; Sakai et al., 1995a).

Phylogenetic studies have elucidated the relationships among taxa in some of the larger Hawaiian lineages (e.g., Baldwin et al., 1991; Baldwin, 2003; Givnish et al., 1995; Wagner & Funk, 1995; Weller et al., 1995; Sakai et al., 1997b; Kim et al., 1998; Ballard & Sytsma, 2000; Baldwin, 2003; Nepokroeff et al., 2003, 2005; Lindqvist et al., 2003; Carlquist et al., 2003; summary in Price & Wagner, 2004). Most Hawaiian groups lack a complete phylogeny, but because of the great isolation and small size of the native Hawaiian angiosperm flora (about 1020 species; Wagner et al., 2005a), it has been possible

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to identify plant lineages descended from a common colonist and examine evolutionary patterns in the Hawaiian Islands with respect to speciation (Price & Wagner, 2004), rarity and conservation status (Sakai et al., 2002), and breeding systems (Sakai et al., 1995a, b). The ability to identify lineages in the extant flora allows examination of traits correlated with breeding systems that are less confounded by phylogenetic relationships than analyses at the species or even the generic level (Sakai et al., 1995a; Steiner, 1988). Based on studies of these lineages, dioecious species in the Hawaiian Islands are descended from dimorphic colonists or from hermaphroditic colonists with in situ evolution of dioecy in the Hawaiian Islands. Ten percent of successful colonists had dimorphic breeding systems and gave rise to lineages with dimorphic species. These dimorphic lineages (with both dimorphic colonists and descendents) account for over half of the dimorphic species. Baker's law suggests that difficulties in obtaining mates will limit colonization by dioecious species more than hermaphroditic species, but the success of dimorphic colonists as well as biogeographic patterns within the Hawaiian Islands suggest that obtaining mates did not severely limit colonization by dimorphic species (Sakai et al., 1995a). The incidence of dimorphism is also high in the Hawaiian Islands because in at least 11 lineages dimorphism evolved from hermaphroditic colonists, accounting for about one third of the current dimorphic species. These lineages, with autochthonous evolution of dimorphism, tended to have higher diversification rates (more species per colonist) than either hermaphroditic lineages or dimorphic lineages (Sakai et al., 1995a). Analysis of lineages also indicates that breeding systems have evolved in the Hawaiian Islands not only in ways that promote outcrossing (e.g., dioecy), but also in ways that promote selfing (Weller et al., 1995; Price & Wagner, 2004, Weller et al., 2005).

While flora-level analyses of factors associated with breeding system evolution reveal general patterns, selective factors promoting speciation and the evolution of dimorphism may be most evident through studies of hermaphroditic lineages that evolved dimorphism after colonization of the Hawaiian Islands. We have focused on *Schiedea* Chamisso & Schlechtendal (Caryophyllaceae), a monophyletic lineage with a hermaphroditic ancestor in which 10 of the 34 species evolved dimorphism in the Hawaiian Islands. *Schiedea* is the fifth largest lineage in the native flora and the most diverse Hawaiian lineage with respect to breeding systems (Weller et al., 1995; Sakai et al., 1997b, Wagner et al., 2005b). We have used a multi-disciplinary approach, including phylogenetic analysis, population biology, and quantitative genetics, to understand both the genetic potential for the evolution of breeding systems in these species and the selective factors that have promoted speciation and shifts in these breeding systems.

Speciation and Phylogenetic Analyses of *Schiedea*

The genus *Schiedea*, with 34 species and 35 taxa, includes deciduous perennials in coastal habitats, sprawling subshrubs in mesic forests, woody shrubs in dry, mesic, and wet forest, rainforest vines, and small subalpine subshrubs. *Schiedea* exhibits the greatest diversity in breeding systems of any native Hawaiian angiosperm genus (Weller et al., 1990; Weller & Sakai, 1990; Weller et al., 1995; Sakai et al., 1997b; Wagner et al., 2005b), including hermaphroditic species that are obligately autogamous, facultatively autogamous, and partially selfing with mixed mating systems, as well as dimorphic species that are gynodioecious (females and hermaphrodites in populations), subdioecious (females, males, and a few hermaphrodites in populations), or dioecious (females and males in populations). In this section we review the changes in biogeography, habitats, and breeding systems that have occurred during diversification of the lineage. Shifts in breeding systems are associated with shifts in habitat and changes in pollination biology in *Schiedea*, and we have used phylogenetic analysis and the comparative method to help infer causal factors in the evolution of breeding systems (Weller & Sakai, 1999).

Earlier phylogenies of *Schiedea* based on morphological characters, chloroplast DNA, and ribosomal DNA restriction-site analysis (Wagner et al., 1995; Weller et al., 1995; Soltis et al., 1996; Sakai et al., 1997b) have been refined more recently using sequence analysis of ITS and ETS genes and a revised and expanded morphological data (Nepokroeff et al., 2005, unpublished). Only extant species were included in the study so that combined analyses could be conducted. Maximum parsimony analyses were performed using unweighted parsimony for the morphology and nuclear (ITS and ETS regions) data, both separately and combined. Maximum likelihood searches on the molecular data utilized an iterative approach to evaluate models and optimize model parameters for an initial set of trees resulting from parsimony analysis, and analyses were then performed under the fully defined model parameters (Nepokroeff et al., 2005). PAUP* v. 4.0b10 (Swofford, 2001) was used for maximum parsimony and maximum likelihood analyses. Bayesian analyses of morphological and molecular data were also conducted (Nepokroeff et al., 2005). The combined molecular and morpho-

logical data sets resulted in 222 characters informative in parsimony analysis. Using equal weighting of characters, 24 most parsimonious trees resulted, with a length of 613. The ITS and ETS sequences yielded a single likelihood tree, and a single Bayesian consensus tree was also produced. These trees were highly congruent in topology with each other and with the parsimony trees and are not shown here. Biogeography, habitat, and breeding system diversity were optimized using MacClade 4.0 (Maddison & Maddison, 2000) onto one of the 24 most parsimonious trees showing the fewest unresolved polytomies, although several weakly supported nodes indicate that conclusions about the number of evolutionary transitions are tentative.

Sequence analysis of ITS, ETS, *mat*K, and *trn*L-F has provided a better understanding of the extant sister group to *Schiedea*. Based on these analyses, the extant sister group to *Schiedea* is strongly supported and consists of a lineage comprised of circumboreal-north temperate *Honckenya peploides* (L.) Ehrh. and *Wilhelmsia physodes* (Fischer ex Seringe) McNeill, a species with an Alaskan to northeastern Asian distribution (Nepokroeff et al., 2005). Analyses of the strict consensus tree of the 24 most parsimonious trees (Fig. 1) indicate that *Schiedea* is a strongly supported monophyletic lineage that arose from a single common ancestor of circumboreal or Alaskan origin. Although much of the phylogeny is only weakly supported, several areas with moderate to strong support are present, including a number of well-supported species pairs. In the strict consensus tree, with the exception of gynodioecious *Schiedea apokremnos* St. John, all other dimorphic species occur in a single moderately well-supported clade (sect. *Schiedea*) that also includes three hermaphroditic species. Within section *Schiedea*, there is moderate support for a terminal subclade of several dimorphic species (*S. salicaria* Hillebrand, *S. ligustrina* Chamisso & Schlechtendal, *S. adamantis* St. John, *S. kealiae* Caum & Hosaka, and *S. spergulina* A. Gray). Unfortunately, this section, which is of greatest interest in the evolution of dimorphism, is also one of the most poorly resolved parts of the tree, perhaps because it has evolved more recently than other clades.

BIOGEOGRAPHY AND PATTERNS OF SPECIATION

About 10% of angiosperm colonists in the Hawaiian flora have temperate affinities, including the ancestor of the lineage comprised of *Schiedea* (Fig. 2; Nepokroeff et al., 2005, unpublished). Although islands have been forming over the Hawaiian hot spot for the past 85 Ma (Clague, 1996), most colonization of the current high islands has occurred within the past 5 Ma, because dispersal between islands was previously limited by an extended period when only small, low, widely spaced islands were formed (Price & Clague, 2002). The current islands with species of *Schiedea* range from the older islands of Nihoa and Kaua'i to the youngest island of Hawai'i (Fig. 3). In this analysis we consider Moloka'i, Lana'i, Maui, and Kaho'olawe as a single island (Maui Nui), because they were interconnected for more than 75% of their existence (Price & Elliott-Fisk, 2004). Species in the most basal clade of *Schiedea* (*S. membranacea* St. John and *S. helleri* Sherff) occur on the older island of Kaua'i, and the sister relationship of these two species is strongly supported. *Schiedea* appears to have colonized the older current major high islands, and the basal clades of *Schiedea* also exhibit the greatest morphological diversity (Wagner et al., 1995). The greater morphological diversity in these older clades may result from diversification into the greater range of environments that develop as islands age and from adaptation to more diverse modes of pollination. The higher probability of extinction of intermediate forms in the older clades may also emphasize differences among species.

Most inter-island colonizations appear to be from older to younger islands (Wagner et al., 1995), but a few back colonizations also may have occurred (e.g., from Kaua'i to Nihoa (*Schiedea verticillata* F. Brown in Christopherson & Caum), from Maui Nui to O'ahu (several dimorphic species), and from O'ahu to Kaua'i (*S. spergulina*)). In most cases, movement between islands led to sufficient isolation in space and time to result in formation of new species that were single-island endemics, rather than species with multi-island distributions. Only three species have multi-island distributions. *Schiedea globosa* H. Mann is a small subdioecious subshrub that grows only on coastal cliffs of O'ahu, Maui Nui, and Hawai'i and may disperse relatively easily between islands by rafting (Wagner et al., 1995); floating mats of *S. globosa* have been observed floating offshore of Moloka'i (Wagner et al., 2005b). Two other species (*S. hookeri* A. Gray and *S. nuttallii* Hooker) are both found on O'ahu and Maui Nui in diverse mesic forest.

Several Hawaiian lineages show inter-island colonization to younger islands followed by habitat diversification (Wagner & Funk, 1995). Species pairs that are well supported in phylogenetic analyses give some indication of the importance and differences in inter-island versus intra-island speciation in *Schiedea*. Most species pairs occurring on older islands are on the same island but differ in habitat, are isolated ecologically, and, in some cases, show pronounced morphological differentiation. Species pairs on younger islands tend to be in similar habitat on different

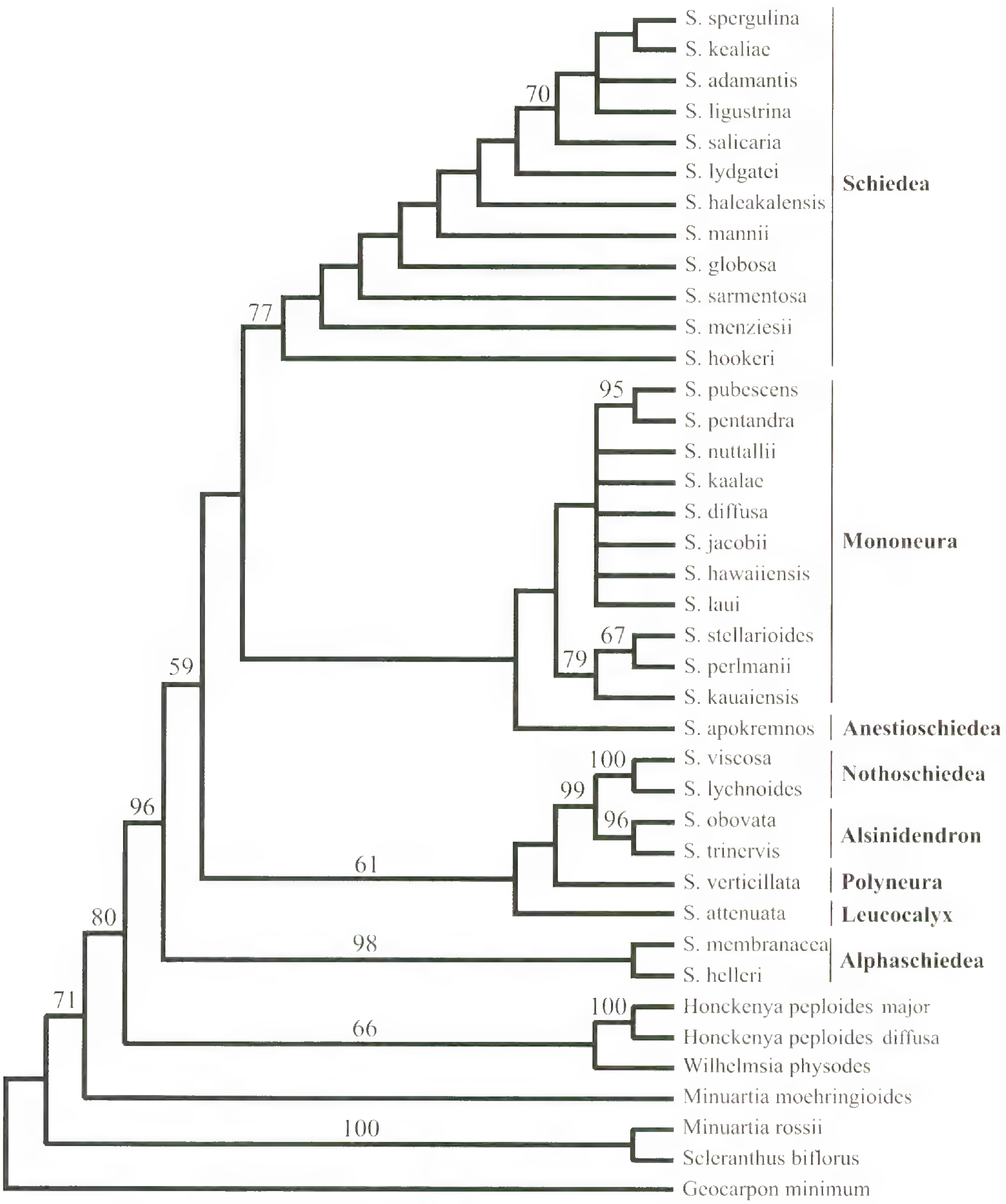

Figure 1. Strict consensus tree of 24 MP trees. Two major partitions of data were analyzed comprising sequence data from nrDNA ITS and ETS regions and morphology. Sixty-one morphological characters were scored, including 13 revised characters published in previous analyses (Weller et al., 1995; Wagner et al., 1995; characters listed in Wagner et al., 2005b). The sections of the genus are shown to the right of each clade. Bootstrap values greater than 50% are shown above the lines. Two extinct species, *Schiedea amplexicaulis* H. Mann and *S. implexa* (Hillebrand) Sherff, are omitted from the analyses (Wagner et al., 2005b). Species for which authorities are not given in the text include *S. haleakalensis* Mattf., *S. mannii* St. John, *S. sarmentosa* Degener & Sherff, *S. kaalae* Wawra , *S. stellarioides* H. Mann, *S. perlmanii* W. L. Wagner & Weller, *S. kauaiensis* St. John, *S. attenuata* W. L. Wagner, Weller & Sakai, *Honckenya peploides* subsp. *major* (Hooker) Hultén (Oregon), *Honckenya peploides* subsp. *diffusa* (Hornemann) Hultén ex V. V. Petrovsky (Baffin), *Minuartia rossii* (R. Brown ex Richardson) Graebner, *Minuartia moehringioides* (DC.) Mattf., *Scleranthus biflorus* Hook.f., *Geocarpon minimum* Mackenzie. Figure adapted from Wagner et al., 2005b.

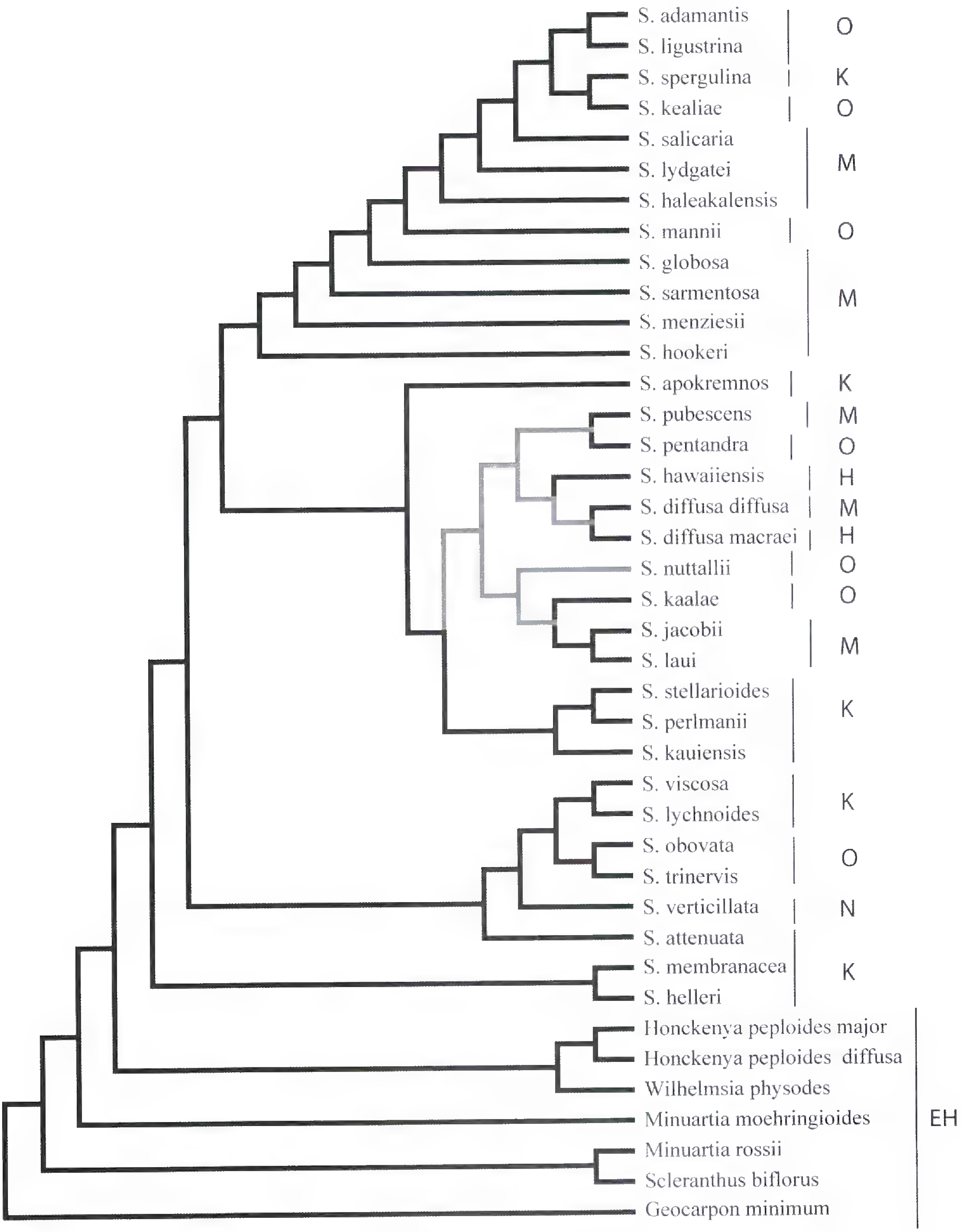

Figure 2. Biogeographic hypothesis for *Schiedea* using one of 24 most parsimonious trees reconstructed with MacClade 4.0 (Maddison & Maddison, 2000; figure adapted from Wagner et al., 2005b). Island abbreviations and ages: Nihoa (N, 7.3 Ma), Kaua'i (K, 4.7 Ma), O'ahu (O, 3.0–2.6 Ma), Maui Nui (M, 2.0–1.2 Ma), Hawai'i (H, 0.6–ongoing Ma), Extra-Hawaiian (EH). For species with multi-island distributions, coding indicates the island where it is most likely that the species evolved. Equivocal regions are indicated in gray.

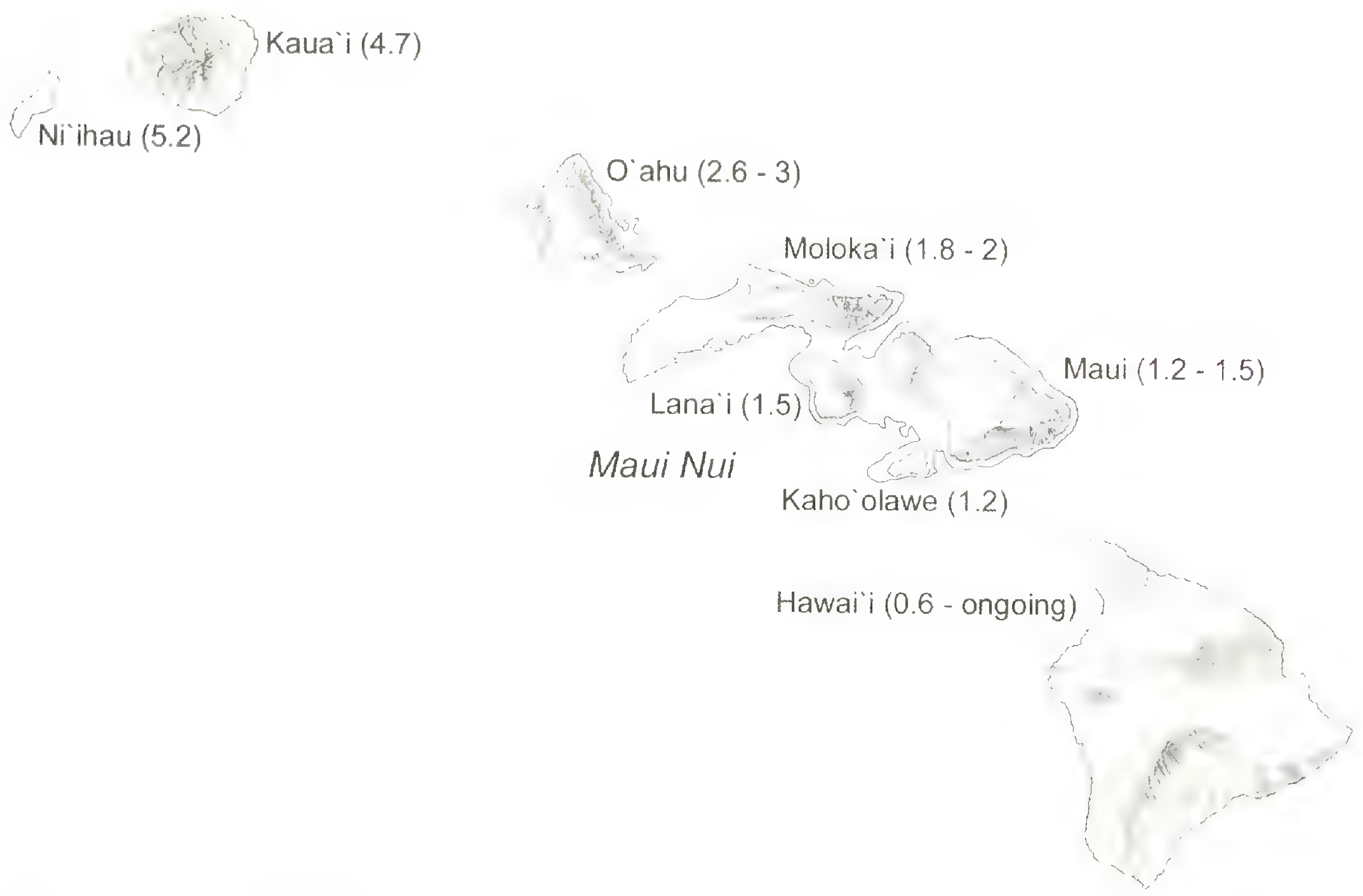

Figure 3. Map of the Hawaiian Islands, with island age in millions of years. Nihoa (7.3 Ma) occurs to the northwest of the islands shown.

islands and show less morphological differentiation. On the older island of Kaua'i, *S. membranacea*, a perennial herb, occurs in the mesic forest of several valleys, while closely related *S. helleri* is a vine found at higher elevations in wet montane forests. In the four species of the former genus *Alsinidendron* H. Mann, inter-island dispersal preceded differentiation in habitat. On Kaua'i, *S. viscosa* H. Mann and *S. lychnoides* Hillebrand are separated by elevation and habitat, although there is some geographic overlap. *Schiedea viscosa* occurs at slightly lower elevations in diverse mesic forest in limited areas, while *S. lychnoides* occurs throughout higher elevation wet forests on Kaua'i. On O'ahu, *S. obovata* (Sherff) W. L. Wagner & Weller occurs in mesic forest at lower elevations throughout the Wai'anae Mountains, while *S. trinervis* (H. Mann) Pax & K. Hoffmann is found only in higher elevation wet forest in the northern Wai'anae Mountains. In the five species pairs on younger islands, both species occur in similar habitats, but geographical isolation has occurred through dispersal to different islands or mountain ranges on the same island (or former island in the case of Maui Nui). Two of these pairs occur in wet habitats (*S. jacobii* W. L. Wagner, Weller & Medeiros and *S. laui* W. L. Wagner & Weller on Maui Nui (Maui and Moloka'i, respectively); the two subspecies of *S. diffusa* A. Gray, *S. diffusa* subsp. *diffusa* and *S. diffusa* subsp. *macraei* (Sherff) W. L. Wagner & Weller on Maui Nui and the island of Hawai'i). One pair occurs in mesic habitat (*S. pentandra* W. L. Wagner & E. Harris and *S. pubescens* Hillebrand on O'ahu and Maui Nui, respectively), and one pair occurs in dry habitats (*S. spergulina* and *S. kealiae* on Kaua'i and O'ahu, respectively). Although both *S. ligustrina* and *S. adamantis* occur on O'ahu in dry habitats, there is clear geographical separation by mountain ranges. *Schiedea ligustrina* occurs throughout the Wai'anae Mountains (formed 3.2–2.5 Ma) in western O'ahu in dry forest to diverse mesic forest, often on cliffs. *Schiedea adamantis* occurs in a single population on steep dry slopes of open shrubland on Diamond Head crater in southeastern O'ahu (formed about 0.5 Ma; Juvik & Juvik, 1998). More definitive biogeographical patterns of other *Schiedea* species await better resolution of their phylogenetic relationships.

Several species may be undergoing directional selection for greater fitness in dry environments colonized relatively recently. For example, *Schiedea hawaiiensis* Hillebrand may have only recently shifted from mesic to dry habitat. It occurs in dry, high light environments, but exhibits morphological traits (large leaves, open pendent inflorescences, vining habit) and physiological traits (maximum levels of photosynthesis, water use efficiency) more characteristic of mesic site species (Mishio et al., unpublished). On younger islands, ecological divergence of species may also be

limited by the later development of geological features creating drier habitats. Wet habitats are present on younger islands as soon as they become high enough to intercept moisture-laden tradewinds, but the drier leeward slopes and cliffs preferred by many *Schiedea* species develop only after erosion and/or subsidence as the islands age (Walker, 1990a, b).

Habitat Shifts and Changes in Breeding System

The spectacular adaptive radiation in breeding systems in *Schiedea* apparently evolved within the past 5–7 million years. The association of changes in breeding system with habitat shifts has made it difficult to discern cause and effect, i.e., to determine if changes in habitat have driven shifts in breeding system, or whether shifts in breeding system have allowed movement into new habitats. Based on character optimization, the ancestor giving rise to *Schiedea* appears to have been hermaphroditic, and the ancestral habitat of *Schiedea* was most likely mesic forest. Although *Honckenya peploides* is dioecious, *Wilhelmsia* Rchb. and other close outgroups are hermaphroditic, and it appears that dioecy was derived independently in *Honckenya* Ehrh. and also within *Schiedea* (Fig. 1; Nepokroeff et al., 2005). Dimorphic breeding systems appear to have been derived independently twice in *Schiedea*—in *S. apokremnos* and once in section *Schiedea*. Within section *Schiedea*, it appears that *S. lydgatei* Hillebrand is hermaphroditic by reversal, possibly through loss of females during colonization of Molokai. Facultative autogamy has evolved three times—once in the former genus *Alsinidendron*, in the species pairs *S. jacobii*–*S. laui*, and in *S. hawaiiensis*–*S. diffusa*. Each of these groups with facultative autogamy has also evolved obligate autogamy (*S. diffusa* subsp. *macraei*, *S. laui*, and *S. trinervis*). Evolution of autogamous breeding systems is also linked to changes in habitat. Diversification into wet habitats has occurred independently five times, and in several of these cases, a shift to facultative or obligate autogamy has occurred. The repeated independent evolution of autogamy with wet habitats may result from historically small population sizes in these species, with selection for closed pendent flowers that are less likely to be adversely affected by extremely wet conditions (Weller et al., 1998; Wagner et al., 2005b). Some exceptions occur to these patterns; *S. helleri* occurs in wet montane forest, but shows no indication of autogamy, and *S. hawaiiensis* occurs in dry forest, but is autogamous rather than sexually dimorphic.

Evolution of dimorphic breeding systems is also linked to changes in habitat (Fig. 4). In both cases, the independent evolution of dimorphism is associated with a shift to dry habitat. All ten dimorphic species occur in dry and windy habitat and most hermaphroditic species occur in mesic to wet habitat. Four hermaphroditic species also occur in dry habitats, although *Schiedea lydgatei* may be hermaphroditic by reversal. This pattern, where all dimorphic species as well as a few hermaphroditic species occur in dry habitats (e.g., *S. menziesii* Hooker, *S. hawaiiensis*, and *S. verticillata*), suggests that the shift to dry windy habitats precedes the shift in breeding system to dimorphism, but that the evolution of dimorphism is not inevitable after a shift to dry habitats. Once the shift in habitat has occurred, selection may simultaneously favor the evolution of dimorphism as a mechanism to promote outcrossing as long as pollen is not limiting for females (Weller et al., 1998). The evolution of adaptations promoting wind pollination becomes critical with the loss of biotic pollination limiting pollen dispersal in these habitats (Rankin et al., 2002). Alternatively, wind-facilitated selfing may evolve because of low pollen production, as in *S. hawaiiensis*, a hermaphroditic dry-site species derived from a lineage of mesic-wet forest species with low pollen production.

Selective Factors in the Evolution of Dimorphism and Selfing

Inbreeding depression, selfing rates, and resource allocation are all factors that can lead to changes in breeding systems by favoring either selfing or, alternatively, the separation of the sexes and the evolution of dimorphism in these species (reviewed in Sakai & Westneat, 2001). In cases with nuclear inheritance of male sterility, as in *Schiedea* (Weller & Sakai, 1991), theoretical models suggest that strong selection for dioecy may occur as a mechanism to promote outcrossing (Lloyd, 1975; Charlesworth & Charlesworth, 1978; reviewed in Geber et al., 1999; Weller & Sakai, 2005). If inbreeding depression (δ) is high, selfed progeny of hermaphrodites will have lower fitness than progeny derived from outcrossing. Unisexual individuals, usually females, will be favored because they produce outcrossed progeny with relatively higher fitness than the selfed progeny of hermaphrodites. Under the simplest conditions, females will be favored if $k + s\delta > 0.5$, where k is the seed production of females relative to hermaphrodites ($k = 0$ if females and hermaphrodites produce equal numbers of seeds) and s is the selfing rate. Because dioecious species produce only unisexual individuals, inbreeding (with selfing as the most extreme form of inbreeding) is much less likely in dioecious species than in hermaphroditic species. Separate sexes may

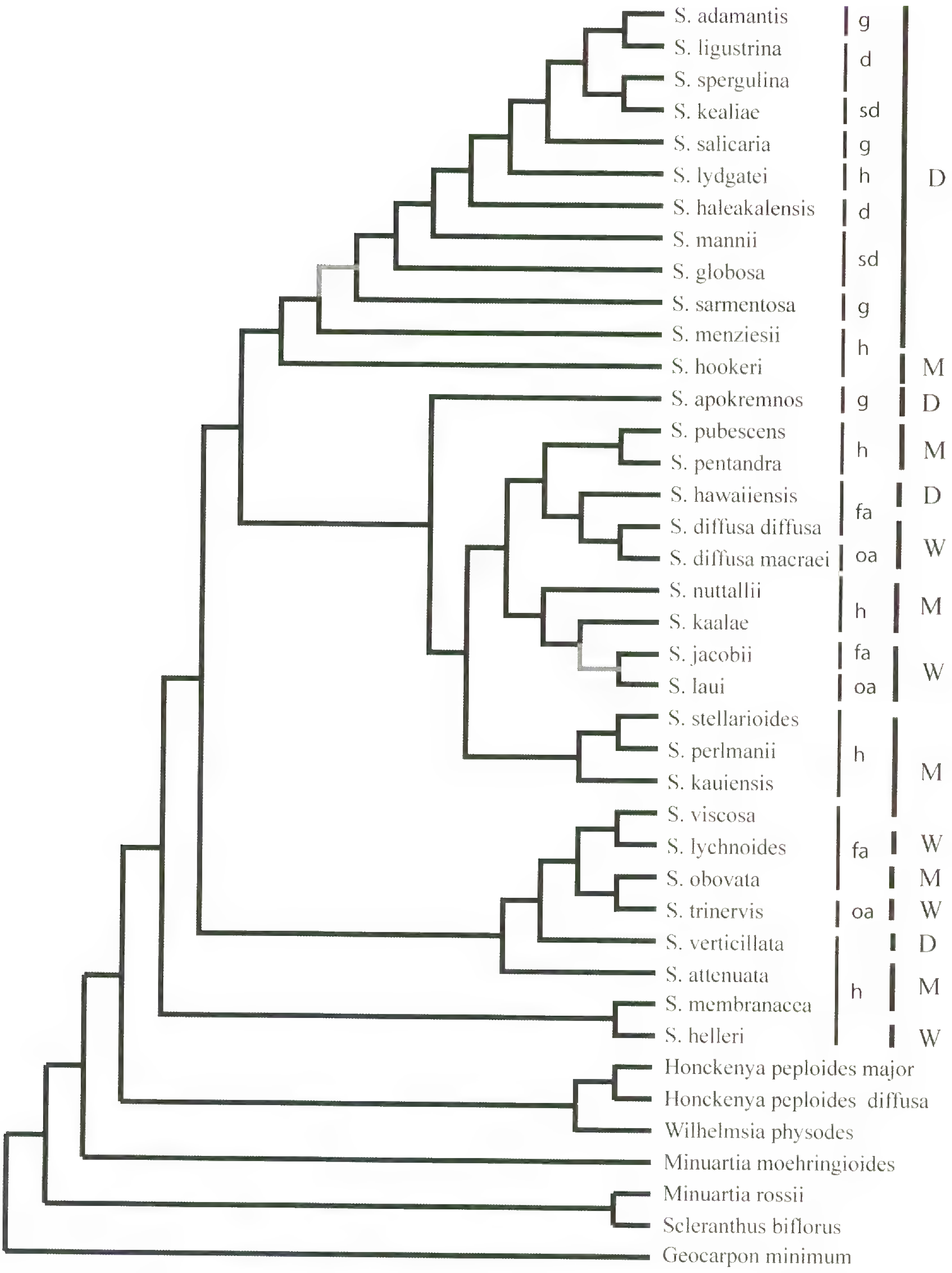

Figure 1. Breeding system evolution hypothesis for *Schiedea* using one of 24 most parsimonious trees reconstructed with MacClade 4.0 (Maddison & Maddison, 2000; modified from Wagner et al., 2005b). Habitats of species are shown in the bar to the right. Equivocal regions for breeding systems are indicated in gray. Habitats: D = dry slopes and cliffs; M = Mesic forest and shrubland; W = Wet forest. Breeding systems: g gynodioecious; d = dioecious; sd = subdioecious; h = hermaphroditic; fa = facultatively autogamous; oa – obligately autogamous.

also be favored in the absence of high inbreeding depression and high selfing rates if females compensate for the lack of male function (pollen production) by producing more than twice as many seeds as hermaphrodites ($k = 1$; Charlesworth & Charlesworth, 1978; Lloyd, 1975). A combination of somewhat greater seed production by females and higher levels of selfing and inbreeding depression may also promote separate sexes.

Resource allocation to primary sex traits such as biomass of pollen and seeds will obviously change with the introduction of unisexual individuals in a population of hermaphrodites (i.e., the evolution of gynodioecy and dioecy from hermaphroditism). The more challenging problem has been to discover if these changes in resource allocation patterns are the driving force in the evolution of separate sexes, with subsequent changes in inbreeding depression and selfing rates, or alternatively, if changes in selfing rates and inbreeding depression occur first. The order of these changes is difficult to deduce in dioecious species, where changes both in resource allocation and in levels of inbreeding and inbreeding depression already have occurred. Gynodioecious species that are under continuing selection for changes in the frequency of females may offer more insights than dioecious species into the factors important in the evolution of both gynodioecy and dioecy.

Comparisons of six species of *Schiedea* species give some clues about the relative order and importance of changes in inbreeding depression, selfing rates, and seed production with the evolution of breeding systems in this lineage (Table 1; Norman et al., 1995, 1997; Sakai et al., 1997a; Culley et al., 1999; Rankin et al., 2002; Weller & Sakai, 2005; Weller et al., 2005). Measurements of seed production were taken from field-collected inflorescences. Selfing rates were measured using starch gel electrophoresis on progeny grown in the greenhouse from field-collected seeds. Because most field sites occur on remote steep cliffs, levels of inbreeding depression were measured in the greenhouse on progeny resulting from controlled crosses involving self and outcross pollinations. Traits used to calculate inbreeding depression included the number of seeds per capsule following the controlled pollinations, percent germination, percent survival until flowering, and either the number of flowers per inflorescence or inflorescence biomass. The relative fitness of selfed progeny as a proportion of values for outcrossed progeny was calculated for each trait for each family and used in a multiplicative fitness function. Inbreeding depression was calculated as 1-relative fitness. Our inbreeding depression studies of these perennial plants in the greenhouse probably underestimate the levels of inbreeding depression expressed in the field over more than one flowering season in presumably harsher field conditions.

Schiedea membranacea is a member of the basal clade of the lineage and has a hermaphroditic breeding system. It is a perennial herb endemic to Kaua'i that grows in mesic environments typical of hermaphroditic species. *Schiedea membranacea* has a high level of outcrossing (low selfing rate) that prevents expression of the high inbreeding depression detected following controlled crosses in the greenhouse (Culley et al., 1999). Measures of genetic diversity (number of alleles per locus, percent of loci polymorphic, and percent heterozygosity) also are consistent with other outcrossing species (Weller et al., 1996). *Schiedea membranacea* is apparently biotically pollinated, with a relatively low pollen : ovule ratio and an open inflorescence (Table 1). Because of the low selfing rate, expression of inbreeding depression is low, and the hermaphroditic breeding system in this species is apparently stable.

In contrast to *Schiedea membranacea*, *S. viscosa* has a stable hermaphroditic breeding system because it has a high selfing rate, but much of the inbreeding depression characteristic of outcrossing species has been eliminated from these populations (Weller et al., 2005). Typical of populations that are historically selfing, the pollen : ovule ratio is extremely low, and *S. viscosa* also has very low measures of genetic diversity (Table 1). *Schiedea viscosa* (formerly in the genus *Alsinidendron*) is a rare hermaphroditic vine that occurs in mesic habitats of Kaua'i. The flowers of *S. viscosa* are pendent and remain relatively closed, traits that may be adaptive in rainy conditions and that may have promoted the evolution of selfing. *Schiedea viscosa* also produces nectar (0.64 µl/flower/24 h in the greenhouse), suggesting an earlier history of biotic pollination (Weller et al., 1998).

Two gynodioecious species illustrate the changes that may occur with an increase in the frequency of females in populations. *Schiedea salicaria*, a gynodioecious species with a low frequency of females (13%), is found in dry windy habitats of the West Maui Mountains. *Schiedea adamantis* is also gynodioecious with a higher frequency of females (39%), and is found on the more recent dry slopes of Diamond Head Crater on O'ahu. In these two species, greater differentiation between females and hermaphrodites in primary and secondary sex traits occurs in *S. adamantis* (Golonka et al., 2005). In *S. salicaria*, females and hermaphrodites show only slight differentiation in floral and inflorescence traits and nearly identical seed production (Weller & Sakai, 2005). In *S. adamantis*, females produce 2.3 times more seeds than hermaphrodites in the field. This occurs because

Table 1. Habitat, breeding system, selfing rate, inbreeding depression, and differences in resource allocation for six species of *Schiedea*. For methods see Norman et al., 1997; Weller et al., 1998; Culley et al., 1999; Rankin et al., 2002; Weller et al., 2005. Resource allocation differences between females and hermaphrodites cannot be calculated in hermaphroditic species. Number of flowers per inflorescence and inflorescence condensation were not measured in *S. viscosa*. Inflorescence condensation is the number of flowers/inflorescence/inflorescence length in cm. Small populations are < 30 individuals; large populations are > 100 individuals. Estimates of genetic diversity (mean number of alleles per locus, percentage of loci polymorphic, and mean heterozygosity) were based on 24 to 39 plants per population (Weller et al., 1996).

Habitat	*S. membranacea* mesic forest herb	*S. viscosa* mesic forest vine	*S. salicaria* dry shrubland shrub	*S. adamantis* dry shrubland shrub	*S. menziesii* dry shrubland shrub	*S. lydgatei* dry shrubland shrub
Breeding system	hermaphroditic	hermaphroditic	gynodioecious (13% F)	gynodioecious (39% F)	hermaphroditic	hermaphroditic (reversal)
Pollinator	biotic	biotic	wind	wind	not adapted to wind	biotic (moth)
Ovule (N)	29	122	35	17	46	32
Pollen (N)	8,037	3,122	14,756	22,177	13,935	11,211
P:O ratio	282	25	419	1308	304	351
Pollen size (μ)	32.5	38.0	33.5	28.7	34.8	32.5
N fl/inflo	94.3	—	30.1	54.5	26.6	24.5
Inflorescence length (cm)	42.3	—	6.9	5.2	4.4	10.6
Inflorescence condensation	2.2	—	4.5	10.5	6.0	2.3
Nectar (μl/24 h)	0.030	0.643	0.236	0.155	0.385	0.325
Selfing rate	low (0.3)	high (presumed 1.0)	high (0.7)	high (0.7)	high (0.8)	low (0.2)
Inbreeding depression	high (0.7)	low (0.0)	high (0.8)	high (0.6)	high (0.8)	high (0.6)
Allocation	—	—	no difference between F and H	F produce 2.3× more seeds than H	—	—
Population size	large	small	large	large	large	large
Mean N alleles/locus	3.0	1.0	2.2	1.6	2.7	2.7
% of loci polymorphic	66.7	0	77.8	22.2	77.8	88.9
Mean heterozygosity	0.366	0	0.305	0.077	0.340	0.322
Assessment	stable; outcrossing hermaphrodites	stable; facultative selfing	unstable; selection for females	unstable; selection for females	unstable; selection for females	stable; outcrossing hermaphrodites

females and hermaphrodites produce similar numbers of inflorescences and flowers per inflorescence in the field, but females produce far more capsules per inflorescence than hermaphrodites (Sakai et al., 1997a). *Schiedea adamantis* also shows much greater adaptation toward wind pollination, with a higher pollen : ovule ratio, smaller pollen grains, and more condensed inflorescence than *S. salicaria*. *Schiedea salicaria*, although wind pollinated, has pollen : ovule ratios, pollen grain size, and inflorescence architecture more similar to biotically pollinated species (Weller et al., 1998; Golonka et al., 2005).

Schiedea salicaria and *S. adamantis* also differ in levels of selfing and inbreeding depression. *Schiedea salicaria* has a mixed mating system, with a high selfing rate (0.7; Weller & Sakai, 2005), but with extremely high inbreeding depression (0.8; Sakai et al., 1989). The low frequency of females in *S. salicaria* is consistent with these estimates, although if selfing and inbreeding depression have been underestimated in these greenhouse studies, selection for increased representation of females may be strong. In contrast, *S. adamantis* has both high selfing rates and high inbreeding depression (Sakai et al., 1997a). In combination with the greater seed production of females, these rates of selfing and inbreeding depression suggest strong selection for females in *S. adamantis*. The predicted frequency of females (based on Lloyd, 1975) is 42%, remarkably close to the observed frequency of 39% (Sakai et al., 1997a). The low estimates of genetic diversity in *S. adamantis* suggest a severe population bottleneck in the past (Weller et al., 1996). More recently, the size of this population has fluctuated widely over the past 20 years, from a high of about 400 flowering plants to a current low of 2 plants because of extended drought and competition from alien species.

Schiedea menziesii, one of the few hermaphroditic *Schiedea* species growing in dry habitats, may be under selection for evolution of sexual dimorphism. Unlike other dry site species, *S. menziesii* does not appear to be well adapted for wind pollination (e.g., low pollen : ovule ratio) and shows no evidence of wind pollination in a wind tunnel (Weller et al., 1998). This species has both high inbreeding depression and high selfing rates, conditions that favor females in populations (Table 1; Rankin et al., 2002). Females occasionally occur in field-collected seeds grown in the greenhouse, but have not been detected in the field. Greenhouse crosses suggest that these females are a result of a mutation for male-sterility (Weller & Sakai, unpublished). Without biotic pollinators, females may not be able to establish and increase in the population without adaptations to wind pollination. The lack of adaptations for intrafloral selfing suggests that the evolution of autogamy is unlikely, even with high selfing rates.

Schiedea lydgatei is another hermaphroditic species found in dry habitats on Moloka'i, and based on phylogenetic evidence, appears to be hermaphroditic by reversal from a sexually dimorphic breeding system. Unlike *S. menziesii*, *S. lydgatei* has a low selfing rate, which limits expression of the high levels of inbreeding depression found in this species. As a consequence, the breeding system is stable despite the high inbreeding depression levels. *Schiedea lydgatei* is apparently moth-pollinated (Norman et al., 1997), and the occurrence of biotic pollination may be critical in the maintenance of high outcrossing rates and hermaphroditism.

The patterns of inbreeding depression, selfing rates, and allocation shifts in these six hermaphroditic and dimorphic species suggest that the evolution of dimorphism is associated with a shift to dry, windy habitats and the evolution of wind pollination in *Schiedea*. The colonization of windy, dry habitats appears to occur before changes in sex allocation. For most hermaphroditic species, the shift to dry, windy habitats apparently is associated with a loss of insect pollinators, resulting in an increase in the selfing rate. The increased selfing rate may result in greater expression of the high inbreeding depression rates found in these historically outcrossing populations. Under these conditions, females could be favored because they are obligately outcrossing, but only if pollination is not limiting populations (Weller et al., 1998). In these environments, the evolution of wind pollination may be followed by the rapid appearance of females in populations. Once females are introduced into the population, there is strong selection for different allocation patterns favoring hermaphrodites with greater male function. In these dry habitats, selection may act on traits associated with wind pollination and/or simultaneously on traits associated with resource allocation to increasingly male or female function.

Genetic Potential for the Evolution of Dimorphism

Theoretical models suggest that the evolution of dioecy may be favored because inbreeding depression levels and selfing rates are both high or because shifts in allocation of resources to a single sexual function result in accelerating fitness returns for individuals (Charlesworth & Charlesworth, 1978; Charnov, 1982; Lloyd, 1984). These accelerating fitness gain curves may result from a variety of ecological factors, including specific dispersal agents and shifts in pollinators (reviewed in Bawa, 1980; Lloyd, 1984; Thomson & Brunet, 1990; Sakai & Weller, 1999). In

Schiedea, shifts to wind pollination, as well as high inbreeding depression and high selfing rates, appear to be strong selective pressures favoring the evolution of gynodioecy and dioecy. The ability to respond to these selection pressures with further evolution of breeding systems will depend upon the genetic potential for changes in allocation to male and female function.

All of these models assume the existence of heritable genetic variation in patterns of allocation to male and female function. Genetic tradeoffs in allocation between the two sexual functions are also assumed (Stanton & Galloway, 1990; Charlesworth & Morgan, 1991; reviewed in Geber et al., 1999). Negative genetic correlations between male and female traits, such as stamen biomass and ovary biomass in hermaphrodites, may enhance the evolution of dioecy, while positive genetic correlations between these traits would impede evolution of dioecy and instead imply selection for larger or smaller flower size.

We know little about patterns of genetic variation and covariation in characters related to sex allocation for natural populations. Only a few recent studies have explored the quantitative genetics of sex allocation traits in hermaphroditic plant species (van Noordwijk & de Jong, 1986; Stanton & Galloway, 1990; Houle, 1991; O'Neil & Schmitt, 1993; Ågren & Schemske, 1995; Delesalle & Mazer, 1995; Mazer & Delesalle, 1996; Campbell, 1997; Mazer et al., 1999). These studies used controlled crosses to create families to estimate genetic variation and covariation of morphological characters, but they generally were not placed in a phylogenetic context. Other studies have examined the quantitative genetics of sex allocation traits in gynodioecious (Ashman, 1999, 2003; Delph et al., 2004, 2005), andromonoecious (Elle, 1998), and dioecious species (Meagher, 1992, 1994). Even fewer studies have examined the quantitative genetics of physiological traits in gynodioecious species (Poot et al., 1996; Caruso et al., 2003).

Closely related species of *Schiedea* with different proportions of females and with variation in male function in hermaphrodites should be especially informative in studies of the genetic changes underlying these sex allocation differences. In *Schiedea*, male sterility is controlled by a single nuclear gene (Weller & Sakai, 1991), but quantitative variation in other traits related to sex allocation in females and hermaphrodites is likely to be controlled by a number of genes. Some gynodioecious species may have breeding systems that are in transition, with allocation patterns that are under directional selection. Given this range of breeding systems and allocation patterns in such closely related species, we expect significant heritability of biomass allocated to male and female function in gynodioecious species. Significant heritability of biomass would indicate the potential for evolutionary change, assuming that genetic correlations do not otherwise constrain the response. We have used a quantitative genetics approach to examine the genetic potential to evolve new breeding systems and traits related to allocation to male and female function in gynodioecious *S. salicaria*, a species with 13% females, and in *S. adamantis*, a species with 39% females.

We used heterozygous hermaphrodites and females as parents to generate families that would produce both hermaphrodites and female progeny. In *Schiedea salicaria*, thirty-five families (each consisting of one heterozygous hermaphrodite and one related female) were used in pollinations to produce the plants for a single generation experiment to estimate the heritabilities and genetic covariances for the focal traits. We employed a partial diallel design similar to that of Meagher (1992), but with larger sample sizes for greater statistical power. Each hermaphrodite was used as a pollen donor and crossed with three females randomly chosen from different families, and each female was crossed with three different unrelated hermaphrodites. In most cases, five females and five hermaphrodites from each sibship were measured for more than 30 traits. Additive genetic variances were estimated separately for females and hermaphrodites by examining the component of variation among paternal half-sib families using restricted maximum likelihood methods (see Kearsey, 1965; Shaw, 1987; Meagher, 1992). Narrow sense heritabilities were calculated for each trait in each sex as the additive genetic variance (four times the paternal variance component for this design) divided by the total variance (paternal variance + maternal variance + error; Falconer & Mackay, 1996). Genetic covariances and correlations were estimated separately for females and hermaphrodites, using best linear unbiased predictors (BLUPs) of sire breeding values obtained from our Proc Mixed analysis (SAS, 2001; Conner et al., 2003). Pearson correlation coefficients between BLUPs were calculated for each sex. The female and hermaphroditic data sets were also combined and Pearson correlation coefficients were calculated between homologous traits of the two sexes.

Heritabilities, and genetic correlations of females and hermaphrodites of Schiedea salicaria. Most floral traits show significant heritabilities in females and hermaphrodites. In general, the floral biomass of stamens (measured only in hermaphrodites) and carpels in both sexes shows high heritability. Fruit biomass is not heritable in terminal flowers, but is heritable in the more numerous lateral flowers in both

sexes (Sakai et al., unpublished). At the inflorescence level, both females and hermaphrodites exhibit high heritability in the number of flowers and fruits per inflorescence (Weller et al., in press). These results suggest that significant genetic variation is present in this species and that a response to selection could result in further differentiation of females and hermaphrodites, depending upon genetic correlations of traits.

Genetic correlations within hermaphrodites are unlikely to promote or hinder the evolution of dioecy in this species. Within hermaphrodites, female biomass (ovary, fruit, or seed) and male (stamen) biomass are independent of each other. Female biomass in females and male biomass in hermaphrodites also showed no genetic correlation, suggesting that specialization toward greater female function in females and greater male function in hermaphrodites would not be constrained. Other genetic correlations may impede selection for sexual dimorphism, with positive genetic correlations between similar traits in females and hermaphrodites. For example, the female biomass of females and of hermaphrodites is significantly genetically correlated, making specialization more difficult (Sakai et al., unpublished).

Schiedea salicaria has likely undergone a recent transition from biotic to abiotic wind pollination, and significant narrow-sense heritabilities were detected for inflorescence condensation and other traits related to wind pollination in *Schiedea* species (Weller et al., in press). Heritabilities were generally higher in hermaphrodites than in females. The presence of significant narrow-sense heritabilities for traits associated with wind pollination suggests that selection for more effective wind pollination in the windy, pollinator-limited environments where *S. salicaria* grows could lead to the evolution of the highly condensed inflorescences characteristic of other wind-pollinated species of *Schiedea*. A recent study of ecophysiological traits of *S. salicaria* and *S. adamantis* showed few differences between females and hermaphrodites, but significant narrow sense heritabilities for stomatal conductance and specific leaf area, suggesting that these traits could also respond to selection (Culley et al., 2006). Further analyses of traits related to floral and inflorescence architecture, wind pollination, and physiology should clarify how other genetic correlations may affect the evolution of dioecy in this species.

Conclusions

A multi-disciplinary approach, including phylogenetic analysis, population biology, and quantitative genetics, has been instrumental in understanding both the genetic potential for different breeding systems to evolve in *Schiedea* and the selective factors that have promoted speciation and shifts in breeding systems. Autogamy and dimorphism evolved independently several times in *Schiedea*, and diversification has been associated with changes in breeding system, pollination system, and habitat. In general, dimorphic species have evolved in dry, windy habitats and are wind pollinated, while autogamous species occur in wetter habitats. Dimorphic breeding systems may have evolved as a mechanism to promote outcrossing because of the expression of high levels of inbreeding depression resulting from high selfing rates that occur with the loss of pollinators related to a shift to drier habitats. Quantitative genetics studies suggest that most morphological traits associated with wind pollination and resource allocation are heritable and could respond to selection. Strong selection for outcrossing in dry habitats and for selfing in wet habitats suggests that a further response to selection in breeding systems and other traits is possible.

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CONTRASTING PATTERNS AND PROCESSES OF EVOLUTIONARY CHANGE IN THE TARWEED–SILVERSWORD LINEAGE: REVISITING CLAUSEN, KECK, AND HIESEY'S FINDINGS[1]

Bruce G. Baldwin[2]

Abstract

Jens C. Clausen, David D. Keck, and William M. Hiesey's biosystematic research on continental tarweeds (Madiinae; Compositae) provided diverse examples of evolutionary change for Clausen's synthesis, *Stages in the Evolution of Plant Species*. Subsequent anatomical work by Sherwin Carlquist demonstrated that the tarweed lineage also includes a spectacular example of adaptive radiation, the Hawaiian silversword alliance. Molecular phylogenetic data and evidence from genetic and hybridization studies have allowed additional perspectives on Clausen et al.'s and Carlquist's hypotheses of tarweed–silversword evolution. In Californian *Layia*, Clausen et al.'s evidence for gradual allopatric diversification for the $n = 7$ taxa accords with patterns of molecular divergence and decay of interfertility across lineages inferred from a rate-constant rDNA tree. In contrast, recent evidence on patterns and timing of diversification in an $n = 8$ *Layia* clade indicates multiple examples of accelerated phenotypic evolution, unresolved by Clausen et al., that evidently reflect rapid "budding off" of morphologically distinct lineages in ecologically novel settings. In rDNA trees of Californian *Holocarpha*, lineages representing different cryptic biological species, documented by Clausen, appear to predate the origin of a morphologically and ecologically distinctive taxon (*H. macradenia* (DC.) Greene) that retains interfertility with relatives of ancestral phenotype; at fine-scale levels of divergence, a disconnect is evident between evolution of intrinsic, post-mating reproductive barriers and phenotypic evolution in *Holocarpha*. Clausen's evidence for strong intersterility barriers between the mostly annual, continental species of the "Madia" lineage contrasts with Gerald D. Carr and Donald W. Kyhos's subsequent finding of partial to full interfertility between the phenotypically disparate, insular species of the Hawaiian silversword alliance, a monophyletic group that descended from continental ancestors in the "Madia" lineage. Molecular phylogenetic data indicating major ecological changes associated with diversification, a brief timeframe for diversification, and a shift to woodiness in the ancestry of the silversword alliance uphold Carlquist's hypothesis of adaptive radiation of the group and help explain the lack of substantial, internal barriers to gene flow across lineages therein. Results of recent investigations have shown that highly dynamic evolutionary change in Madiinae, both in phenotypic characters and in modes and patterns of diversification, extends to even finer-scale evolutionary levels than indicated by Clausen et al.'s elegant studies. In general, current evidence on diversification in Madiinae appears to be consistent with Clausen et al.'s views concerning the importance of ecological factors in incipient evolutionary divergence. Phylogeny of Madiinae is no longer the intractable problem perceived by Clausen; relatively little is known about the biological basis for the extreme evolutionary propensities of tarweeds.

Key words: Adaptive radiation, cryptic diversity, diversification, edaphic endemism, *Holocarpha*, *Layia*, *Madia*, Madiinae, peripheral isolates, reproductive isolation, speciation.

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Contrasting modes of diversification (speciation) have been suggested to explain evolutionary change within different lineages of subtribe Madiinae (Compositae), a monophyletic plant group of 119 species commonly known as tarweeds (see Baldwin, 2003a). The name "tarweed" belies the great morphological and ecological breadth of plant life encompassed by Madiinae, especially by the Hawaiian silversword alliance, a famous example of adaptive radiation (see Baldwin, 2003b, c). The Californian or continental tarweeds, in general, are less diverse ecologically than the silversword alliance but contain about three-fold more recognized species and have been under evolutionary investigation far longer than have the Hawaiian taxa. A recent book, *Tarweeds & Silverswords: Evolution of the Madiinae (Asteraceae)*, includes extensive reviews on natural history, morphological and taxonomic diversity, chromosome evolution, hybridization, glandular structures, leaf and wood anatomy, secondary chemistry, molecular evolution, conservation genetics, evolutionary relationships, and processes of diversification in Californian and Hawaiian Madiinae (Carlquist et al., 2003).

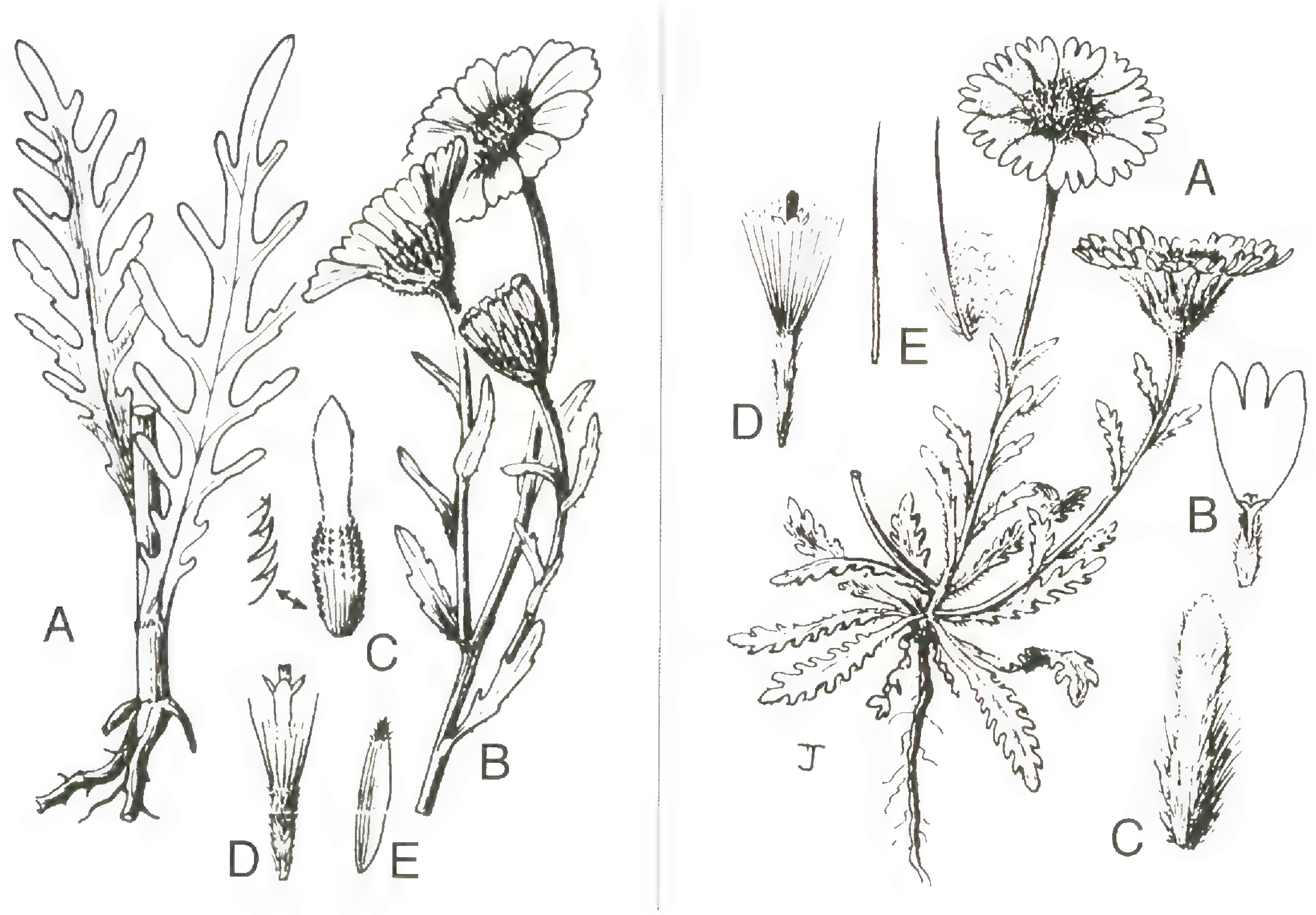
The first evolutionary studies of tarweeds began at the Carnegie Institution of Washington at Stanford, California, with pioneering biosystematic investigations by Harvey Monroe Hall and E. B. Babcock on *Hemizonia* DC. (Babcock & Hall, 1924) and by Hall and his two junior colleagues David D. Keck and William M. Hiesey on various lineages of Madiinae (Hall, 1932). Hall recruited Danish plant evolutionist Jens Clausen to join the research team at the Carnegie Institution in 1931; Clausen assumed the position of principal researcher four months later, following Hall's untimely death in 1932, and pursued decades of tarweed research there as leader of the renowned Clausen, Keck, and Hiesey team (see French, 1989).

Clausen, Keck, and Hiesey are best known for their reciprocal transplant studies along Hall's (1932) west-east ecological transect of California (e.g., Clausen et al., 1940, 1948), which helped establish the importance of local adaptation in explaining variation in widespread plant species. Less widely appreciated are Clausen, Keck, and Hiesey's broader interests in understanding how diversity arises in plants and their extensive experimental studies on Californian tarweeds. In his synthesis, *Stages in the Evolution of Plant Species*, Clausen (1951) showed that plant groups recognized by taxonomists as species represent a wide diversity of evolutionary entities that can differ greatly in relative levels of morphological, ecological, and genetic divergence and can arise by distinct processes. Californian tarweeds constitute about half of the evolutionary examples presented by Clausen in his 1951 book, which has been a major inspiration for generations of Madiinae researchers.

Here, I revisit some of Clausen, Keck, and Hiesey's hypotheses of evolutionary change in Madiinae and evolutionary hypotheses of subsequent tarweed researchers who, at least in part, based their studies on previous work by one or more members of the Carnegie team. Addition of a molecular phylogenetic framework has proven useful for re-evaluating previously suggested modes of diversification in various groups of Madiinae, bearing in mind the limitations of phylogenetic data for inferring such evolutionary processes (see Losos & Glor, 2003). In light of data from those recent and ongoing studies, I suggest that the contrasts in processes of tarweed evolution so well documented by Clausen, Keck, and Hiesey in comparisons across genera are far more extensive than earlier appreciated. In addition, new molecular perspectives demonstrate that phylogenetic structure in Madiinae extends to finer-scale levels than previously suggested, in part probably reflecting divergence of ecologically distinct lineages that conform, at least in some measure, to Clausen et al.'s (1939, 1940, 1948) ecotype concept.

Evolutionary Contrasts between Major Lineages of *Layia*

Gradual allopatric divergence in the n = *7* Layia *lineage.* A widely studied hypothesis of diversification in the California tarweeds considered by Clausen, Keck, and Hiesey concerns the group of taxa in *Layia* Hook. & Arn. ex DC. with seven pairs of chromosomes. Members of *Layia* are spring ephemerals that sometimes have white-tipped ray corollas and are commonly called "tidy-tips" (Figs. 1, 2; see Baldwin, 2003b, c). Clausen et al. (1941) investigated the evolution of *Layia* extensively, in part by examining crossability and interfertility among all members of the genus. Their crossing diagram for *Layia* (Fig. 3) illustrates the intrinsic potential for gene flow estimated from seed set and extent of chromosome pairing in F_1 hybrids. Clausen et al. (1941) regarded taxa with seven pairs of chromosomes, on the left side of the figure, as constituting one of two "major blocks of species" in *Layia*, which in turn was subdivided into three, informal "complexes," each united by morphological characteristics and moderate levels of interfertility: (1) *L. chrysanthemoides* (DC.) A. Gray and *L. fremontii* (Torr. & A. Gray ex A. Gray) A. Gray, (2) *L. jonesii* A. Gray, *L. leucopappa* D. D. Keck, and *L. munzii* D. D. Keck, and (3) *L. platyglossa* (Fisch. & C. A. Mey.) A. Gray. Stebbins (1949: 232) regarded the interfertile taxa in



Figures 1 and 2. Widely sympatric, ± intersterile members of *Layia* with seven pairs of chromosomes. Figure 1 (left). *Layia chrysanthemoides*. —A. Base of plant. —B. Capitulescence. —C. Involucral bract (abaxial view). —D. Disk floret. —E. Receptacular bract. Figure 2 (right). *Layia platyglossa*. —A. Habit. —B. Ray floret and enfolding involucral bract (adaxial view). —C. Involucral bract (abaxial view). —D. Disk floret. —E. Pappus elements (two forms).

each of the first two complexes as "species in the state of becoming."

Stebbins (1966) showcased Clausen, Keck, and Hiesey's (1941) biosystematic data on the members of *Layia* with $n = 7$ as exemplary of gradual, allopatric divergence (see also Stebbins, 1982). Stebbins (1966) noted that taxa of *Layia* with moderate interfertility are invariably allopatric; in contrast, taxa that are sympatric are moderately to highly intersterile, with reduced chromosome pairing at meiotic metaphase I in F_1 hybrids (Fig. 4). Under the assumption that degree of interfertility reflects recency of common ancestry (a risky premise; see Donoghue, 1985), the patterns shown in Figure 4 are consistent with the hypothesis that sympatric taxa underwent earlier divergence from a common ancestor compared to allopatric taxa or populations in each of the three subgroups, and that sympatry is secondary, following a period of lineage divergence in geographic isolation. Warwick and Gottlieb (1985) re-examined the hypothesis of gradual, allopatric divergence among the $n = 7$ members of *Layia* from the perspective of allozymes. Their results mirrored the findings of Clausen, Keck, and Hiesey (1941) and the scenario outlined by Stebbins (1966) by showing highly reduced genetic similarities in pairwise comparisons among the three subgroups relative to genetic identities within each group.

A molecular phylogenetic perspective on diversification of the $n = 7$ members of *Layia* based on nuclear ribosomal DNA (rDNA) internal transcribed spacer (ITS) sequences (Fig. 5; Baldwin, 2003a, unpublished) reinforces the evolutionary conclusions of Clausen et al. (1941), Stebbins (1966), and Warwick and Gottlieb (1985). Monophyly of the $n = 7$ group is well supported, as are each of the three subgroups ("complexes") proposed by Clausen et al. (1941). The tree topology and branch-lengths correspond well to Clausen et al.'s (1941) model of gradual, allopatric diversification, with sympatric taxa being deeply divergent relative to allopatric members of each subgroup and in comparison to lineages in the ($n = 8$) sister-group to the $n = 7$ lineage. The results provide no evidence of accelerated loss of interfertility within any part of the $n = 7$ group, wherein internal barriers to gene flow may well reflect byproducts of gradual evolutionary divergence. Not shown in Figure 5 is the finding (Baldwin, un-

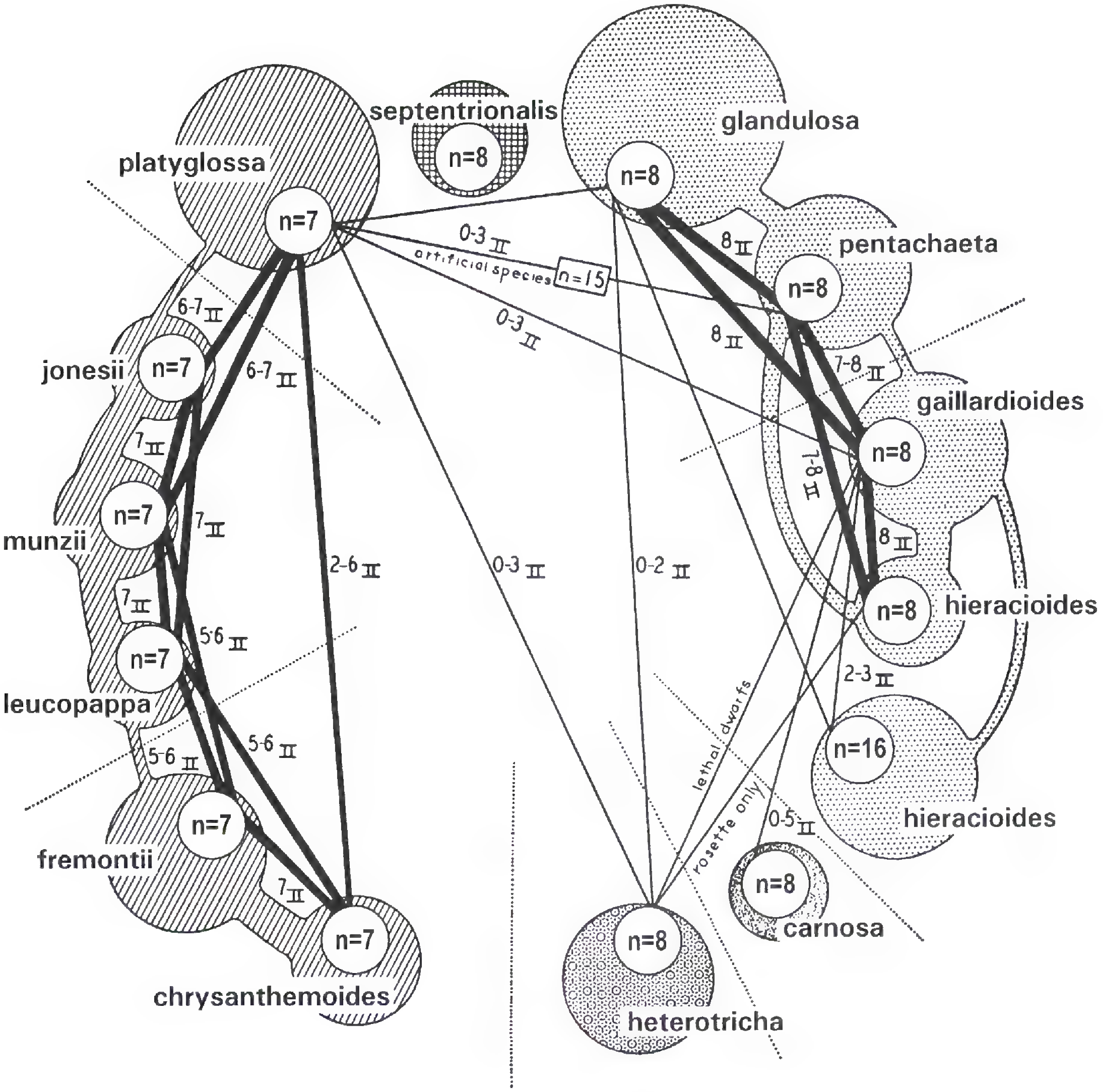


Figure 3. Crossing diagram of *Layia*, adapted from Clausen, Keck, and Hiesey (1941). Circles represent different species; size of circles roughly illustrates relative abundance of each species. Width of shaded connections between species indicates estimated intrinsic potential for gene flow based on seed set in F_1 hybrids. Width of lines connecting species indicates degree of chromosome pairing at meiotic metaphase I in F_1 hybrids; number(s) of meiotic chromosome pairs in F_1 hybrids or vegetative condition of non-flowering hybrids are presented along lines. Dotted lines between species or groups of species indicate major discontinuities in morphological variation. Used by permission of the publisher, Carnegie Institution of Washington.

published) that rDNA sequences from different, often widely separated populations of each species were resolved within a common, monophyletic lineage, as expected under Clausen et al.'s (1941) evolutionary model.

The $n = 7$ lineage of *Layia* evidently conforms to Clausen's view of the "most normal pattern of speciation," with "a more or less simultaneous and gradual separation in morphologic, ecologic, genetic, and cytologic characteristics" (Clausen, 1951: 90). Groups that exhibit approximately rate-constant divergence of characteristics across lineages present minimal problems for systematists; even application of phenetic criteria should provide accurate reconstructions of relationships under such conditions (see Felsenstein, 2004). These attributes are putatively reflected by congruence between Clausen et al.'s (1941) phylogenetic hypotheses for the $n = 7$ *Layia* group (based on essentially phenetic considerations of morphological similarity, chromosome-number similarity, and levels of meiotic chromosome pairing and interfertility) and clades resolved from molecular

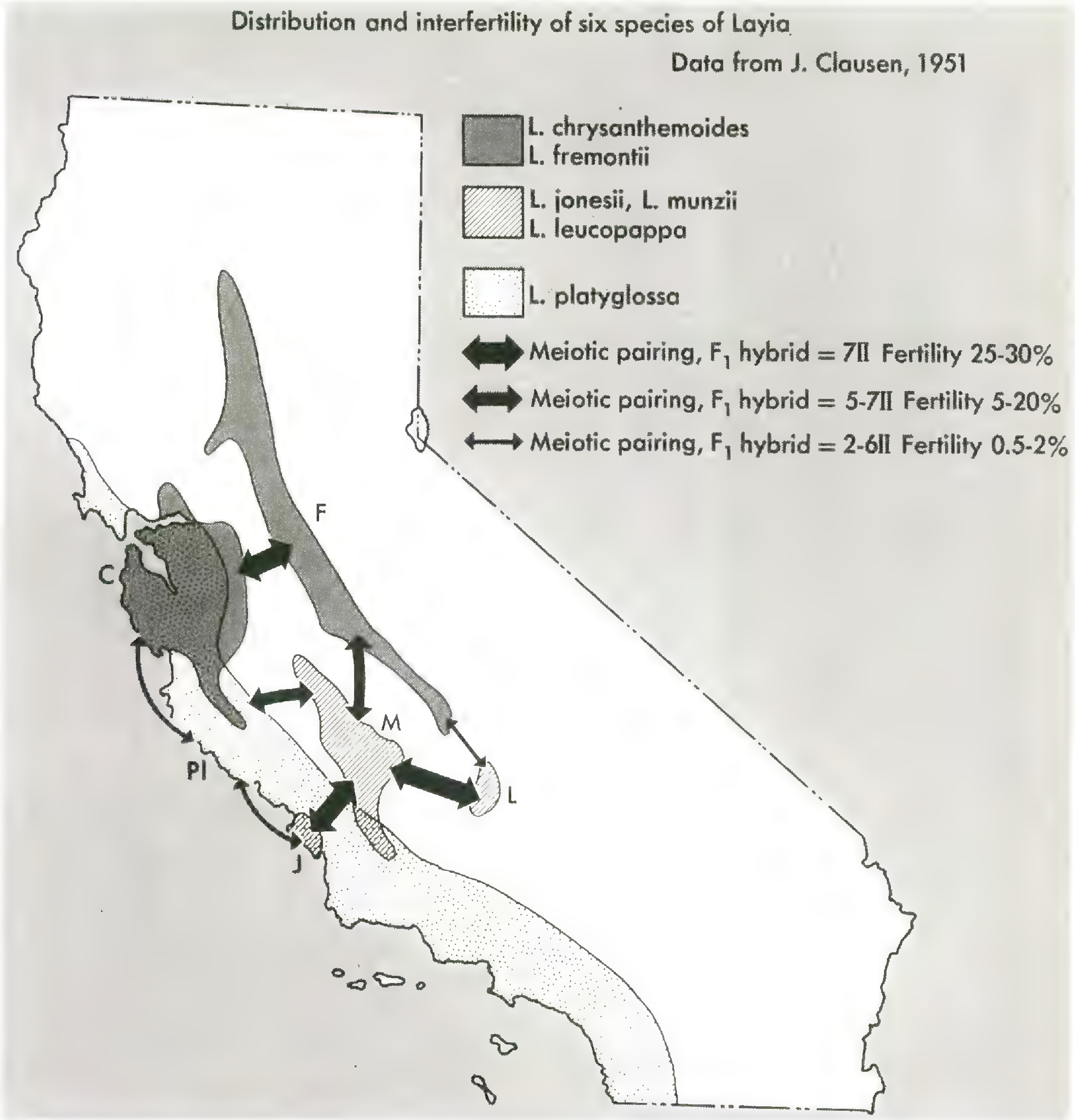


Figure 4. Distributions and interfertilities of species of *Layia* with seven pairs of chromosomes. Letters alongside species distributions correspond to the first letter(s) in species epithet of those taxa (C = *L. chrysanthemoides*; F = *L. fremontii*; J = *L. jonesii*; L = *L. leucopappa*; M = *L. munzii*; Pl = *L. platyglossa*). Note moderate to high interfertility of most allopatric species and low interfertility of widely sympatric species. Reprinted from Stebbins (1966), by permission of Pearson Education, Upper Saddle River, New Jersey.

phylogenetic analyses. As noted above, the three n = 7 "species complexes" proposed by Clausen et al. (1941) correspond precisely to clades 1–3 in Figure 5; in addition, Clausen (1951: 129–130) indicated that "*Layia platyglossa* is almost a species complex in itself... It is genetically sharply separated from *chrysanthemoides* and *Fremontii* and... is more closely related... to... *leucopappa*, *Munzii*, and *Jonesii*", in complete conformity with the rDNA tree topology (Figure 5).

Accelerated phenotypic divergence in n *= 8* Layia *lineages.* In contrast to evidence for gradual, allopatric divergence in the n = 7 *Layia* lineage, experimental and molecular data from the congeneric n = 8 sister-lineage have revealed multiple examples of taxa that likely arose rapidly in peripheral or otherwise isolated, ecologically distinct settings. Phylogenetic and phenotypic patterns and timing of diversification resolved in two n = 8 sublineages are similar, at least in part, to expected outcomes of

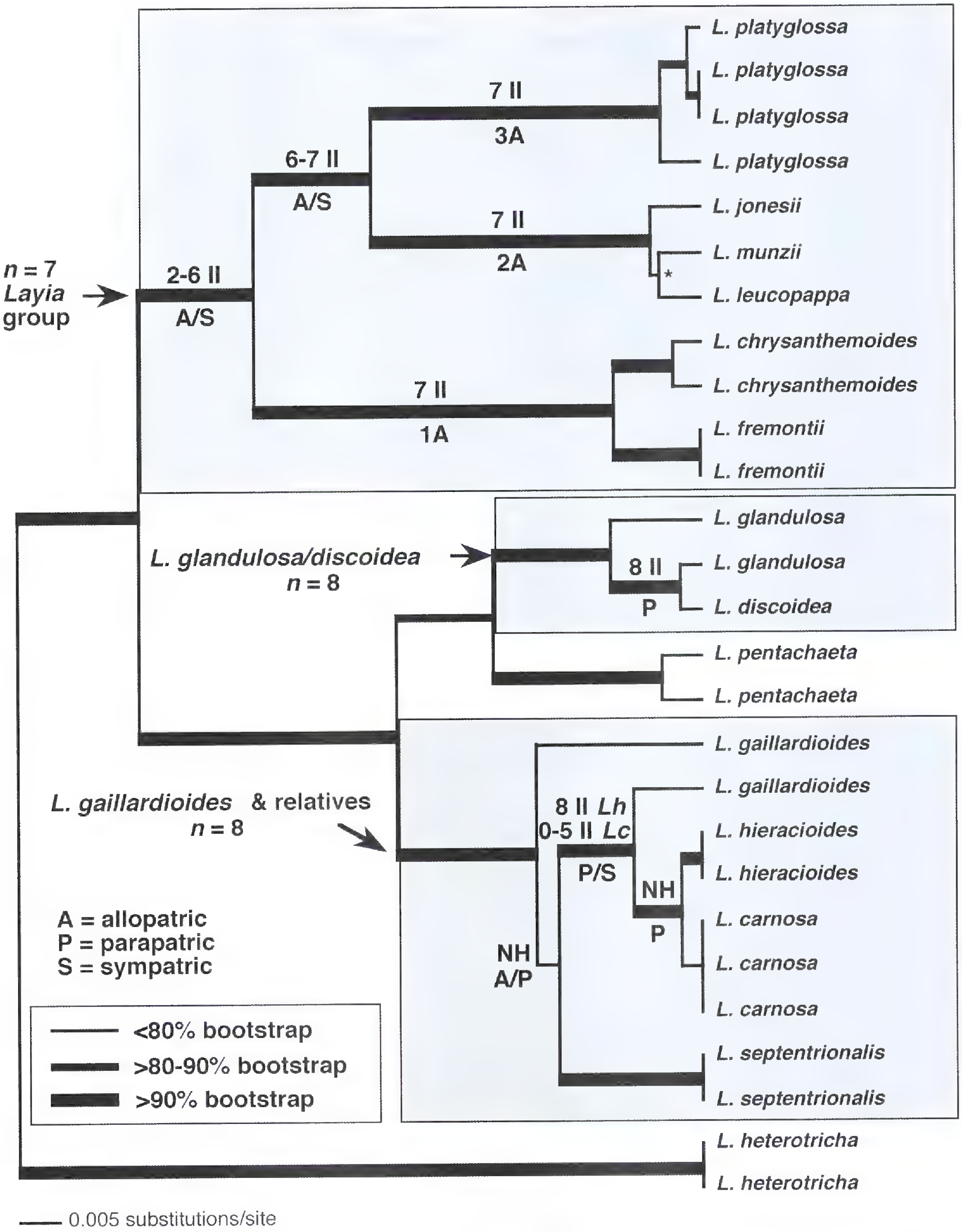
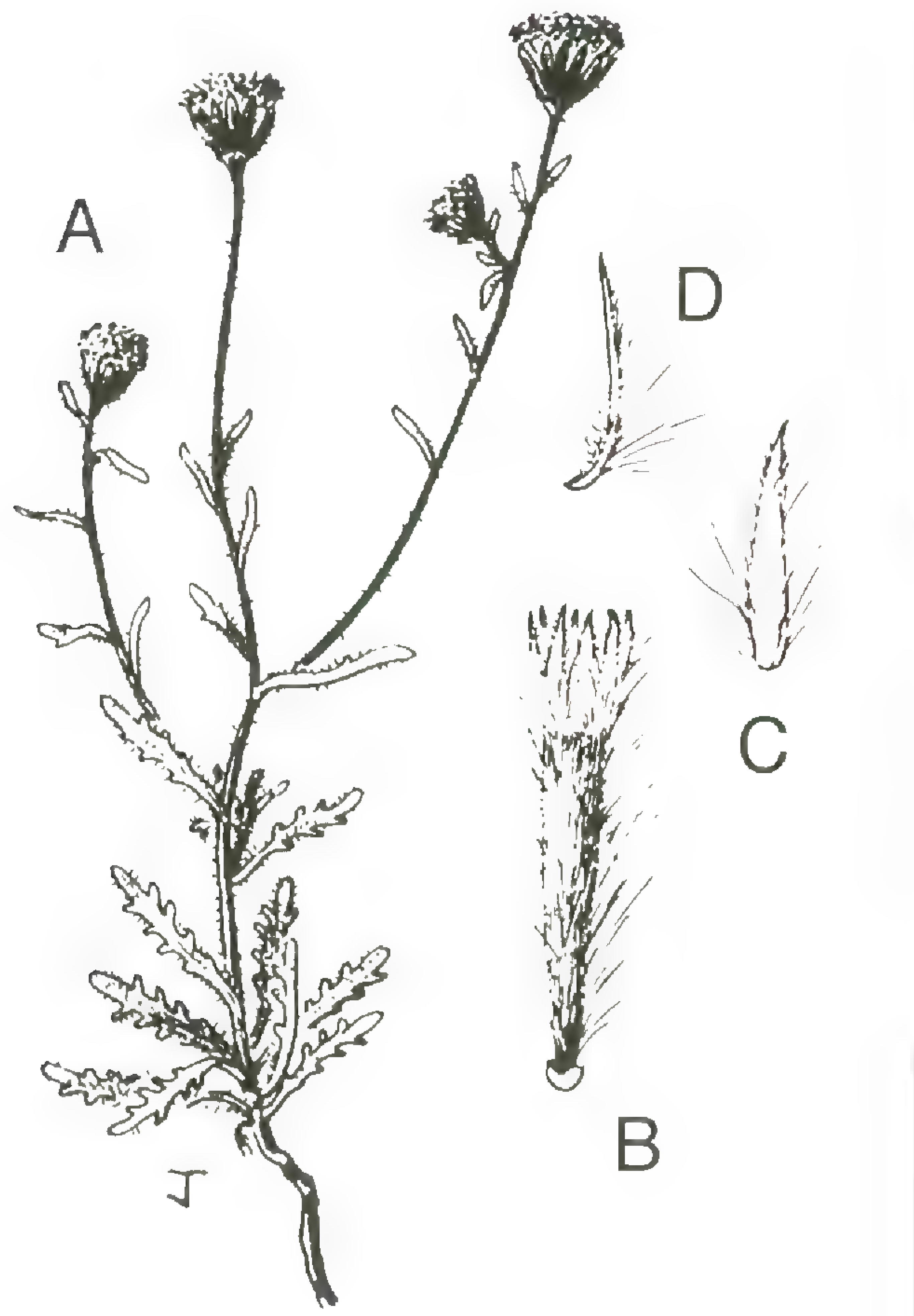
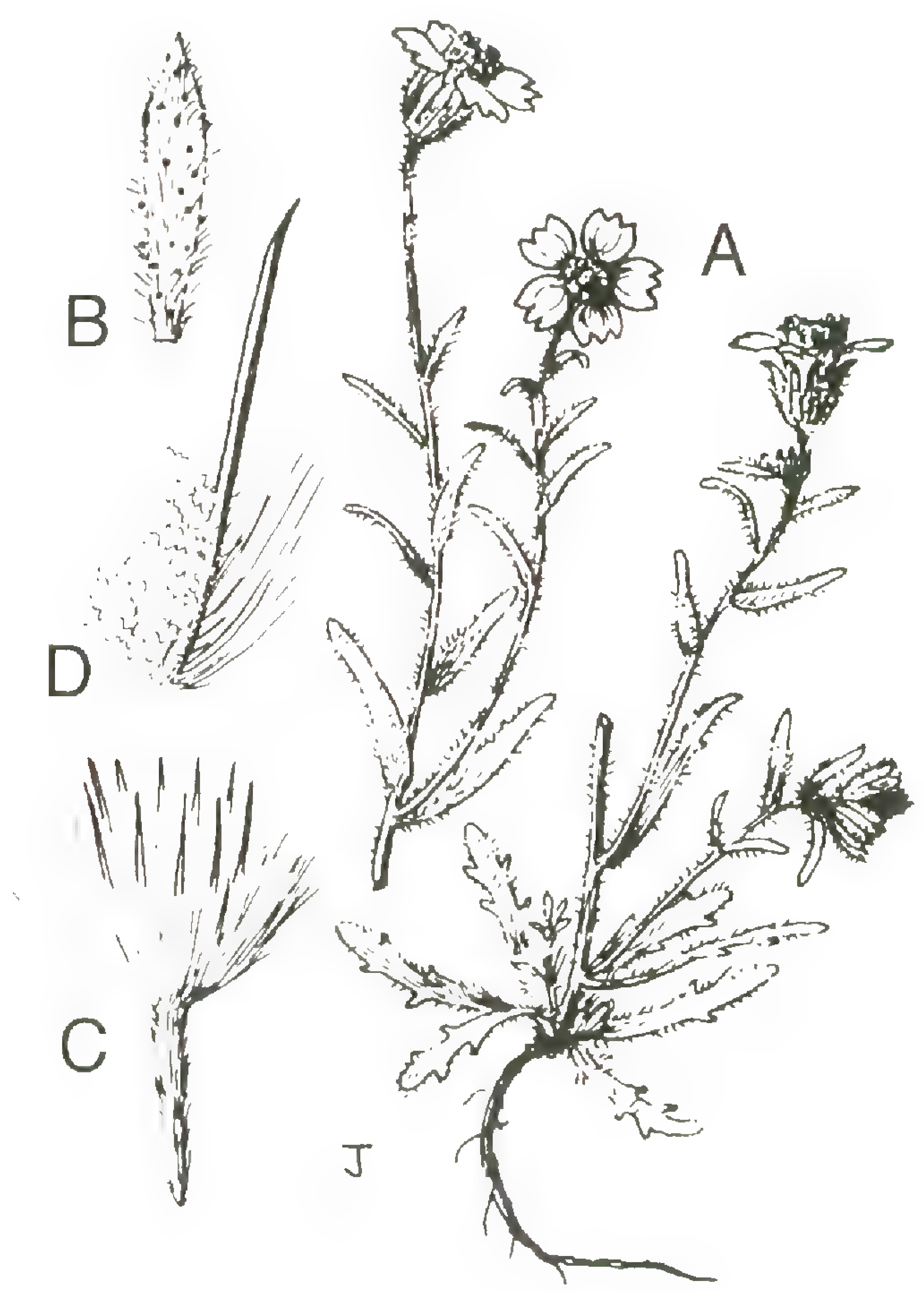


Figure 5. Phylogenetic hypothesis for *Layia* based on nuclear 18S 26S rDNA internal transcribed spacer sequences (Baldwin, 2003a, unpublished); one of two maximally parsimonious trees (* = clade unresolved in strict consensus tree). Branch lengths correspond to relative time since divergence, under maximum-likelihood optimization; rate constancy of ITS evolution across lineages could not be rejected using Felsenstein's (1988) likelihood-ratio test. In the $n = 7$ group, clades 1A, 2A, and 3A represent Clausen et al.'s (1941) three "complexes" of allopatric species, discussed in the text. Numbers of meiotic chromosome pairs in F_1 hybrids between taxa in a clade are indicated above branches (Lh = hybrid with diploid *L. hieracioides*; Lc = hybrid with *L. carnosa*; NH = no hybrids reported), based on Clausen et al.'s (1941) crossing data for *Layia* (see Fig. 3). The tree was rooted using *Arnica mollis* Hook., *Hulsea algida* A. Gray, *Raillardella pringlei* Greene, and *Adenothamnus validus* (Brandegee) D. D. Keck as the outgroup. Terminal taxa of the same name represent geographically disjunct populations. See Appendix 1 for authorship of species names not mentioned in text.





Figures 6 and 7. Ecologically distinct, interfertile members of *Layia* with eight pairs of chromosomes. Figure 6 (left). *Layia discoidea.* —A. Habit. —B. Fruit with pappus. —C. Pappus element (abaxial view). —D. Pappus element (lateral view). Figure 7 (right). *Layia glandulosa.* —A. Habit (bisected). —B. Involucral bract. —C. Fruit with pappus. —D. Pappus element (lateral view).

peripatric speciation (Mayr, 1982), quantum evolution (Simpson, 1944), or quantum speciation (Grant, 1963, 1971; Lewis, 1966), as discussed below.

Evolutionary divergence on a local geographic scale in general has been widely suggested to be of major importance in plant evolution (e.g., Ehrlich & Raven, 1969; Levin, 1993), although convincing phylogenetic evidence for a putatively common pattern of local diversification, i.e., "budding off" of distinctive, new lineages from within a relatively uniform set of related lineages, is usually lacking in studies of suspected "progenitor–derivative" species pairs (see Gottlieb, 2004). Expected paraphyly of a widespread "progenitor" species relative to a "derivative" isolate in some models of local diversification may fail to be resolved in phylogenetic analyses because of insufficiently high rates of evolution in the characters under study, extinction or inadequate sampling of populations (see Neigel & Avise, 1986), or gene flow among lineages within the paraphyletic progenitor taxon (e.g., for genes under strong selection; see Rieseberg & Burke, 2001). Based on various theoretical considerations, Rieseberg & Brouillet (1994) suggested that paraphyly of plant species may be common. Gottlieb (2004) listed 31 examples of species pairs in plants that represent putative examples of lineages wherein one species descended from ancestors in another; he discussed evidence for budding-off of three annual, diploid species of angiosperms, including an $n = 8$ member of *Layia*, *L. discoidea* D. D. Keck.

The best-studied hypothesis of rapid evolution among the $n = 8$ *Layia* taxa concerns the origin of *L. discoidea* (Fig. 6), which is morphologically so unusual that it was not initially recognized to be a tarweed—and was about to be described in a monotypic genus ("Roxira," for co-discoverers Roxana S. Ferris and Ira L. Wiggins)—until Clausen et al. (1941) observed some similarities with tarweeds and subsequently found that the plant was completely interfertile with *L. glandulosa* (Hook.) Hook. & Arn. (Fig. 7). Despite being fully interfertile, *L. glandulosa* and *L. discoidea* differ greatly in morphology and ecology. For example, like most tarweeds, *L. glandulosa* has ray florets and involucral bracts; *L. discoidea* lacks both ray florets and true involucral bracts, with marginal receptacular bracts constituting a false involucre. The two taxa also differ substantially in features of the pappus. *Layia glandulosa* occurs mostly in coarse, sandy soils, including sand dunes,

in semi-arid and montane regions of California and the western deserts; *L. glandulosa* has the widest distribution of any obligate outcrosser in Madiinae (see Baldwin, 2003b, c). *Layia discoidea* is confined to serpentine barrens in a small region of the Inner South Coast Ranges of California (San Benito and western Fresno counties). Serpentine erodes to clay (structurally unlike the sandy habitats of *L. glandulosa*), has a high magnesium/calcium ratio unfavorable for most plants, is low in some essential plant nutrients, and contains concentrations of heavy metals that can be toxic to angiosperms (see Kruckeberg, 2002). Approximately 9% of minimal-rank vascular plant taxa (species, subspecies, and varieties) endemic to the California Floristic Province are confined to serpentines (Kruckeberg, 1992) and have been interpreted either as products of recent, *in situ* evolution (neoendemics) or as evolutionary relicts (paleoendemics) that became secondarily restricted to serpentine habitats, possibly by competition or interference with other taxa, in association with late Cenozoic climatic changes (see Raven & Axelrod, 1978).

On the basis of morphological and ecological considerations, Clausen (1951: 82) concluded that *Layia discoidea* was "probably an edaphic race (of *L. glandulosa*) adapted to the serpentine soil, and possibly an ancient relict." Clausen et al. (1947: 121) were unable to resolve the relationship between the two taxa: "There is no way of determining which race was first, the rare, inconspicuous one from the serpentine (*L. discoidea*), or the common, showy one from sandy habitats (*L. glandulosa*)."

In the 1980s, Gottlieb and colleagues revisited the origin and age of *Layia discoidea*. Gottlieb et al. (1985) found that genetic similarity between *L. discoidea* and *L. glandulosa*, based on allozymes, was almost as high as values typical of conspecific plant populations. They concluded that the serpentine endemic *L. discoidea* represents an example of a peripheral isolate that diverged relatively rapidly and recently in an ecologically marginal setting from an ancestor referable to the geographically widespread *L. glandulosa*. Ford and Gottlieb (1989, 1990) corroborated Clausen et al.'s (1947) conclusion that only two major genes are responsible for presence or absence of ray florets and associated involucral bracts in *L. glandulosa* and *L. discoidea* and showed that morphological differences between the two taxa are controlled by "a complex admixture of genes with large and small, qualitative and quantitative effects" (Ford & Gottlieb, 1990: 44).

In the ITS trees for *Layia* (Fig. 5), resolution of a clade comprising *L. discoidea* and *L. glandulosa* corroborates Clausen et al.'s (1947) hypothesis that the two phenotypically dissimilar taxa constitute a natural group. Strong support for the nested placement of *L. discoidea* within *L. glandulosa* corroborates Gottlieb et al.'s (1985) hypothesis that *L. discoidea* descended from a lineage of *L. glandulosa*. Gottlieb et al.'s (1985) additional conclusion that *L. discoidea* represents an example of relatively recent evolution is also evident from the ITS tree; the branch separating *L. discoidea* from the most closely related lineage of *L. glandulosa* in the rate-constant ITS tree is comparable or shorter in length to branches of conspecific sequences in other members of *Layia*, e.g., *L. pentachaeta* A. Gray, the sister-species to *L. glandulosa* and *L. discoidea*.

A more extensive phylogenetic analysis of relationships within the *Layia glandulosa*/*L. discoidea* lineage based on expanded sampling of populations and sequences, with combined ITS and ETS (external transcribed spacer) data, yielded a nearly noise-free tree that reinforces support for recent descent of *L. discoidea* from a sublineage of *L. glandulosa* (Baldwin, 2005). Sequences of the five populations of *L. discoidea* sampled are identical; sequences of *L. glandulosa* are heterogeneous and are resolved as a grade of lineages that are geographically distinct and, to some extent, morphologically divergent. For example, the sister-group to all other lineages in the *L. glandulosa*/*L. discoidea* clade is a morphologically and ecologically discrete group endemic to coastal sand dunes. Phenotypic disparity among the lineages of *L. glandulosa* is minimal, however, compared to morphological and ecological differences between *L. discoidea* and relatives in *L. glandulosa*. Fine-scale patterns resolved in the ETS+ITS tree are consistent with Ford and Gottlieb's (1990) conclusion that yellow-rayed populations of *L. glandulosa*, sometimes treated as *L. glandulosa* subsp. *lutea* D. D. Keck, are the closest relatives of *L. discoidea*, which lacks ray florets but has one or more modifier gene(s) for yellow ray-corolla color; most populations of *L. glandulosa* have white ray corollas and all but one of the sampled white-rayed populations are resolved, based on the molecular data, as more distantly related to *L. discoidea* than are the sampled yellow-rayed populations.

As noted by Gottlieb (2004), the evolutionary origin of *Layia discoidea* did not involve the major genotypic effects predicted under quantum speciation (Grant, 1981); complete interfertility with *L. glandulosa* and the highly contrasting edaphic settings of the two taxa implicate ecological selection without radical genetic reorganization in divergence of *L. discoidea*, in keeping with some recent, general views on accelerated evolution in peripheral populations (e.g., Barton & Charlesworth, 1984; Coyne, 1994). Mayr's (1982: 5)

Figure 8. *Layia gaillardioides* ($n = 8$). —A. Stem segment. —B. Capitulescence, with peduncle detail. —C. Involucral bract (abaxial view). —D. Involucral bract (lateral view). —E. Ray floret (adaxial view). —F. Disk floret. —G. Pappus element (lateral view).

refinement of his earlier ideas on rapid divergence of peripheral isolates or founders ("peripatric speciation") allowed for the possibility of "rapid change... due more to greatly increased selection pressures... than to the genetic consequences of inbreeding," in closer accord with the proposed evolutionary scenario for *L. discoidea*. Proximity of potential habitats of *L. glandulosa* and *L. discoidea* even leaves open the possibility that divergence of *L. discoidea* may have occurred in the presence of potential for gene flow with *L. glandulosa*, although adjacency of populations of the two taxa has not been documented and no evidence of hybridization is apparent from the rDNA sequences.

A less widely studied example of rapid evolutionary change among the $n = 8$ *Layia* taxa concerns *L. gaillardioides* (Hook. & Arn.) DC. (Fig. 8) and close relatives. Clausen (1951: 16) regarded the extensive interpopulational variation in ray corolla color, vegetative morphology, and flowering time within *L. gaillardioides* as "very spectacular." In part based on common-garden studies, he concluded that some variation among populations of *L. gaillardioides*, e.g., in leaf margins (Fig. 9), is heritable and follows a west–east geographic pattern "correlated with ecological differences between the outer and inner Coast Range" (Clausen, 1951: 14–15). Phylogenetic analysis of rDNA sequences of *Layia* corroborates Clausen's (1951) suggestion that west–east interpopulational differences in *L. gaillardioides* reflect genetic divergence, though at a deeper evolutionary level than he proposed. Four major, allopatric evolutionary lineages within *L. gaillardioides* are well supported by rDNA data and three of the four lineages replace one another from west to east through the Coast Ranges (Baldwin, unpublished).

The four semi-cryptic, allopatric lineages of *Layia gaillardioides* do not constitute a clade in rDNA trees: the morphologically and ecologically distinct *L. carnosa* (Nutt.) Torr. & A. Gray, *L. hieracioides* (DC.) Hook. & Arn., and *L. septentrionalis* D. D. Keck are nested among lineages of *L. gaillardioides* and appear to represent examples of accelerated phenotypic divergence from *L. gaillardioides*-like ancestors (Baldwin, unpublished; Fig. 5 includes representatives of three of the four major lineages of *L. gaillardioides*). *Layia carnosa* (Fig. 10), a rare endemic of outer coastal foredunes, occupies a marginal ecological setting where *L. gaillardioides* does not occur. A hypothesis that *L. carnosa* arose as a peripheral isolate at the coastal-most limits of a widespread progenitor is consistent with distributions of the two closest relatives of "beach layia": (1) a lineage of *L. gaillardioides* that occurs along windward slopes of the North Coast Ranges and San Francisco Bay Area and (2) *L. hieracioides* (Fig. 11).

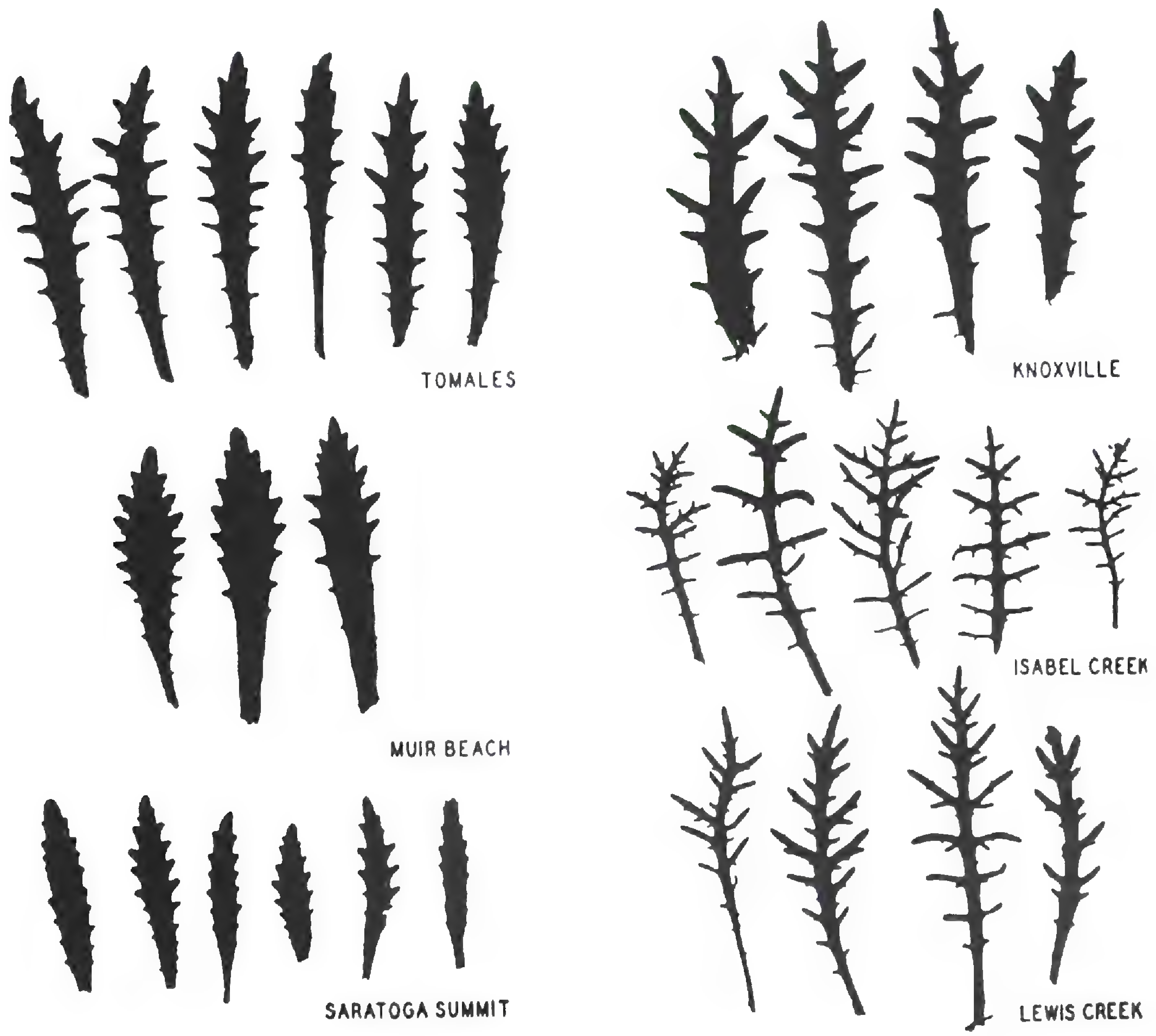
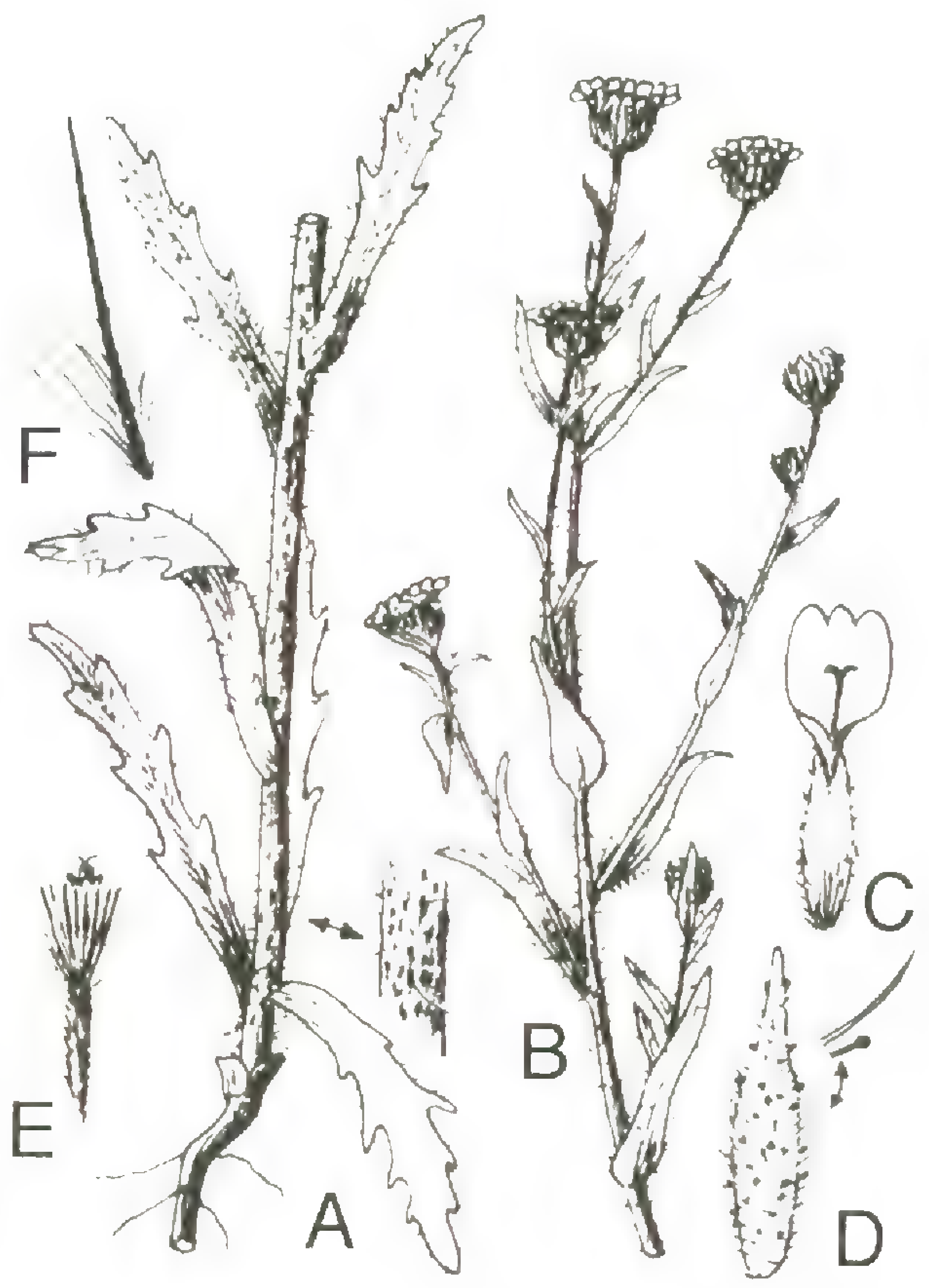


Figure 9. Basal-leaf variation within and among six populations of *Layia gaillardioides*. Each leaf represents a different individual grown under common-garden conditions at Stanford. Three populations from the outer Coast Ranges of California are represented at left; three populations from the inner Coast Ranges of California are represented at right (top-to-bottom equates to north-to-south distribution of populations). Note deeper leaf-lobing in populations from the drier, hotter interior of the state. Reprinted from *Stages in the Evolution of Plant Species*, by Jens Clausen. Copyright © 1951 by Cornell University. Used by permission of the publisher, Cornell Univ. Press.

which occurs widely in the South Coast Ranges, in part on sandy soils and even coastal backdunes. Self-compatibility in *L. carnosa* and *L. hieracioides* (Clausen, 1951)—otherwise unknown in *Layia*—is associated with some conspicuous morphological differences from other members of the *L. gaillardioides* clade (e.g., reduced sizes of ray corollas and heads). The putative shift toward a more highly inbreeding mating system in the self-compatible taxa can be reasonably suspected to have promoted evolutionary change, as suggested by Gottlieb (1973) for origin of the self-compatible *Stephanomeria malheurensis* Gottlieb (Cichorieae; Compositae), a well-studied example of local, rapid phenotypic divergence from self-incompatible ancestors (see Gottlieb, 2004). *Layia septentrionalis*, the other taxon nested among lineages of *L. gaillardioides* in the rDNA trees (Fig. 5), is an obligately outcrossing, narrowly distributed plant of poor, sandy or serpentine soils that occurs in interior regions of the North Coast Ranges, where populations of one major lineage of *L. gaillardioides* occur sporadically; the two taxa have not been reported to occur together.

Parallels between patterns of evolutionary change in the *L. gaillardioides* assemblage and the *L. glandulosa/L. discoidea* lineage, discussed above, do not extend to patterns of interfertility. In contrast to complete interfertility between members of *L. glandulosa* and *L. discoidea*, members of *L. gaillardioides* are largely to completely intersterile with members of *L. carnosa* and *L. septentrionalis* and are largely interfertile with diploid members of *L. hieracioides* (Fig. 3; Clausen, 1951; Baldwin, unpublished). Consideration of the observed interfertility patterns



Figures 10 and 11. Self-compatible taxa in *Layia* with eight pairs of chromosomes. Figure 10 (left). *Layia carnosa*. —A. Habit. —B. Involucral bract (abaxial view). —C. Ray floret (adaxial view). —D. Disk floret. —E. Pappus element. Figure 11 (right). *Layia hieracioides*. —A. Proximal stem, leaves, and roots. —B. Capitulescence. —C. Ray floret and enfolding involucral bract (adaxial view). —D. Involucral bract (abaxial view). —E. Disk floret. —F. Pappus element.

in a phylogenetic context leads me to conclude that *L. carnosa* and *L. septentrionalis* underwent accelerated evolution of intrinsic, post-mating reproductive barriers, as expected with quantum speciation (Grant, 1971), although no evidence of chromosome repatterning has been detected in *Layia* (Clausen, 1951), unlike in such well-studied, plant examples of quantum speciation as *Clarkia lingulata* Harlan Lewis & M. Lewis (Lewis & Roberts, 1956; see Gottlieb, 2004) and *Stephanomeria malheurensis* (Gottlieb, 1973, 2004). Clausen (1951: 130) concluded that *L. carnosa* and *L. septentrionalis* each represents a "monotypic species complex," largely based on intersterility or lack of crossability with other layias. In addition, Clausen et al. (1941) regarded *L. carnosa* as highly divergent morphologically from other species or groups of species in *Layia* (Fig. 3). The major morphological discontinuity between *L. carnosa* and other members of *Layia* perceived by Clausen, Keck, and Hiesey now appears to reflect accelerated morphological evolution in *L. carnosa*, as documented in the origin of *L. discoidea* (Ford & Gottlieb, 1990), rather than a distant evolutionary relationship with other members of the same genus.

The $n = 8$ *Layia* clade encompassing *L. glandulosa*/*L. discoidea* and the paraphyletic *L. gaillardioides* and relatives stands out in *Layia* as an exceptional example of how levels of interfertility or morphological divergence can be misleading about phylogeny, unlike in the $n = 7$ *Layia* clade, where an evidently different mode of evolutionary divergence led to congruent patterns of interfertility, morphological similarity, and relationship. Whether such stark contrasts between the $n = 7$ and $n = 8$ sister lineages in patterns of evolutionary change are attributable to intrinsic or extrinsic factors in the history of the two groups remains unknown. The principal conclusion that has emerged from molecular phylogenetic research previewed here is that evolutionary processes in *Layia* have been more dynamic than was evident based on Clausen et al.'s (1941) biosystematic data alone. Evidence for multiple instances of accelerated phenotypic divergence in *Layia* underscores the potential importance of peripherally isolated populations in plant evolution (see Rieseberg & Brouillet, 1994; Gottlieb, 2004). For systematists, the possibility that diversification is often marked by major changes in rates of phenotypic evolution and rates of decay of

interfertility across lineages, as inferred for the principal $n = 8$ *Layia* clade, makes risky a reliance on phenetic considerations for estimating relationships or circumscribing taxa, as noted earlier (e.g., Donoghue, 1985).

Cryptic Biological Species and Rapid Phenotypic Evolution in *Holocarpha*

As noted by Clausen (1951: 94): "There is one genus of the tarweeds of California which differs strikingly from the pattern of speciation in *Layia* of the same subtribe of the Compositae in that it has very strong barriers of sterility even between neighboring populations of one species. These populations are so similar in external appearance that they cannot be distinguished. This genus is *Holocarpha*." *Holocarpha* Greene also differs greatly from *Layia* in ecology. For example, members of *Layia* escape summer drought by flowering and fruiting during the wet spring months; most members of *Holocarpha* tolerate summer drought and flower in summer and fall (see Baldwin, 2003b, c).

Clausen (1951) emphasized that reproductive isolation in plants can be achieved by different means. He provided examples of "groups having predominantly ecological barriers" (e.g., physiological/habitat differences), "predominantly morphological differentiation" (e.g., in floral features associated with pollination), and "predominantly genetic barriers" (Clausen, 1951: 90–107) in opposition to "more typical species" wherein "the pattern of development...from ecological races is through small steps involving the genetic and chromosome systems and the morphological characters" (Clausen, 1951: 107). Clausen's (1951) main example of diversification dominated by the evolution of genetic barriers to gene flow across lineages was *Holocarpha*, a tarweed genus with four taxonomic species (recognized on the basis of morphological characteristics and chromosome numbers) and an indefinite number of unrecognized, cryptic biological species.

Clausen, Keck, and Hiesey's experimental studies in *Holocarpha* revealed that interpopulational crosses within each of two widespread, taxonomic species, *H. heermannii* (Greene) D. D. Keck and *H. virgata* (A. Gray) D. D. Keck, were either unsuccessful or yielded inviable or sterile hybrids (Fig. 12; Clausen, 1951). Chromosomal studies revealed karyotypic differences between intersterile, often morphologically indistinguishable plants from different populations (Fig. 13; Clausen, 1951). Clausen (1951: 99) concluded that chromosome evolution via structural rearrangements had resulted in each population of *H. heermannii* and *H. virgata* becoming "a breeding unit by itself and genetically sharply separated from its neighbors." Hybrids between members of *H. virgata* (Fig. 14) and a rare species, *H. macradenia* (DC.) Greene (Fig. 15), exhibited modest fertility, in contrast to intersterility between members of different "conspecific" populations of *H. virgata*. Palmer (1982) conducted additional cytogenetic and morphological studies in *Holocarpha* that extended Clausen's (1951) characterization of patterns of interfertility and chromosomal evolution in the genus.

An ongoing molecular phylogenetic study of *Holocarpha* (Baldwin, unpublished) has revealed evidence of a disconnection between evolutionary divergence in conspicuous morphological and ecological characteristics and the origin of intrinsic, postmating reproductive barriers in the group. Well-supported rDNA trees based on ITS and ETS sequences have confirmed that each of the three widespread species recognized by Clausen, Keck, and Hiesey, i.e., *H. heermannii*, *H. obconica* (J. C. Clausen & D. D. Keck) D. D. Keck, and *H. virgata*, descended from distinct ancestors; the rare *H. macradenia* descended from an ancestor within (paraphyletic) *H. virgata* (Fig. 16). Detailed comparisons of the relative timing of evolutionary changes in *Holocarpha* are now possible because of minimal noise in the molecular dataset, phylogenetic structure both among and within recognized species, and inability to reject rate constancy of molecular evolution across lineages using Felsenstein's (1988) likelihood-ratio test.

Based on branch-length comparisons across the rate-constant rDNA trees, divergence of the highly distinctive *Holocarpha macradenia* from an ancestor within *H. virgata* was more recent than evolutionary divergence of some cryptic, intersterile lineages within *H. virgata* (Fig. 16; Baldwin, unpublished). Recent origin of *H. macradenia* is consistent with modest interfertility between *H. macradenia* and some populations of *H. virgata*, in contrast to strong intersterility barriers between most studied populations of *H. virgata* (Clausen, 1951; Palmer, 1982). In short, extensive morphological and ecological evolution of *H. macradenia* was not accompanied by development of intersterility with closely-related members of *H. virgata*; conversely, evolution of intersterility between "conspecific" lineages within *H. virgata* (and *H. heermannii*) was accompanied by relatively minor or insubstantial phenotypic divergence, despite longer evolutionary timeframes for such divergence to have occurred compared to the relatively rapid rise of *H. macradenia*.

Based on available data, *Holocarpha macradenia* appears to represent yet another example among continental tarweeds of a peripheral isolate that underwent rapid morphological and ecological di-

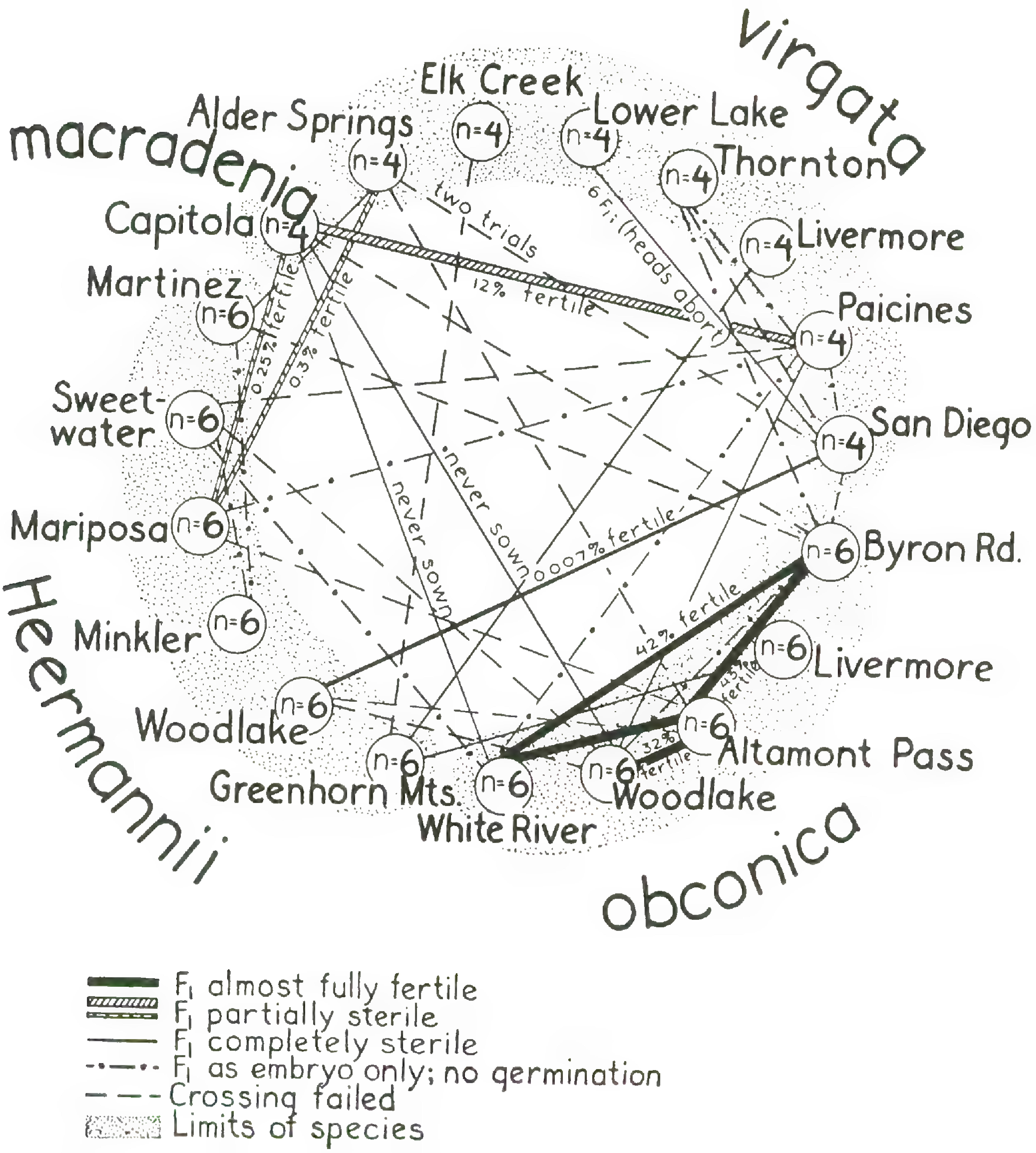


Figure 12. Crossing diagram of *Holocarpha*. Note strong, postmating reproductive barriers between "conspecific" populations in *H. heermannii* and *H. virgata*, high interfertility among populations of *H. obconica*, and partial fertility of hybrids between *H. macradenia* and *H. virgata*. Reprinted from *Stages in the Evolution of Plant Species*, by Jens Clausen. Copyright © 1951 by Cornell University. Used by permission of the publisher, Cornell Univ. Press.

vergence in a novel habitat. Unlike other members of *Holocarpha*, which are found extensively in interior or southern Californian habitats with extremely dry, hot summer climates, *H. macradenia* occurs on coastal terraces in the San Francisco Bay and Monterey Bay areas, where summer drought and temperatures are greatly ameliorated by onshore winds and fog. Clausen (1951: 105) suggested that *H. macradenia* and *H. virgata* "...probably were interconnected as maritime and inland races of one species before the Coast Ranges arose." He further posited that the rise of the Coast Ranges "...provided the dry interior habitats now so completely exploited by the three interior species" (Clausen, 1951: 105). Palmer (1982, 1987) suggested instead that *H. macradenia* arose from members of *H. virgata* that invaded the coastal region during an unusually warm period within the last 10,000 years. He based his hypothesis in part on patterns of chromosome evolution and interfertility within and between the two taxa and on morphological considerations, including a suggestion by Carlquist (1959a: 305) that distinctive distal-leaf morphology of

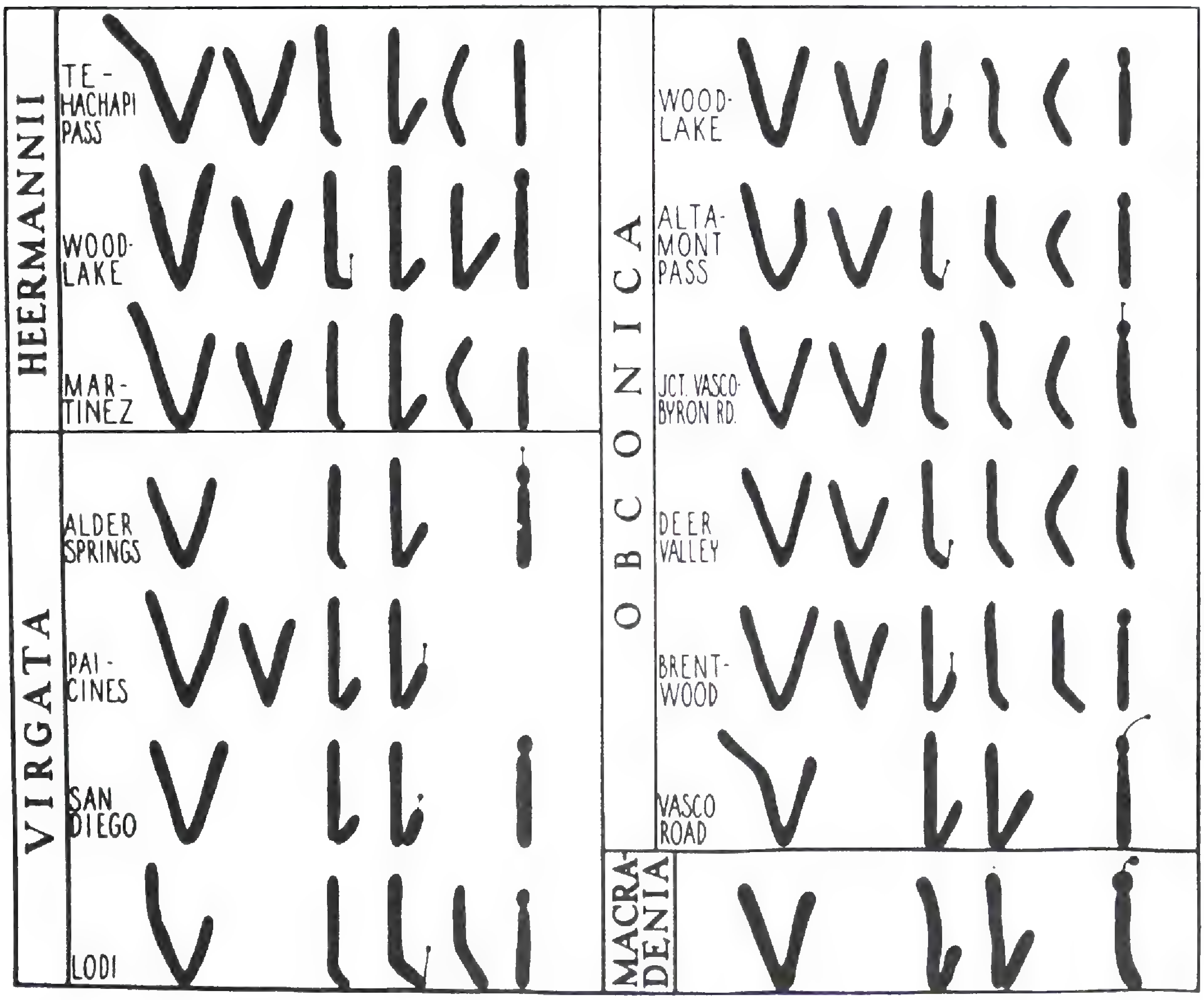


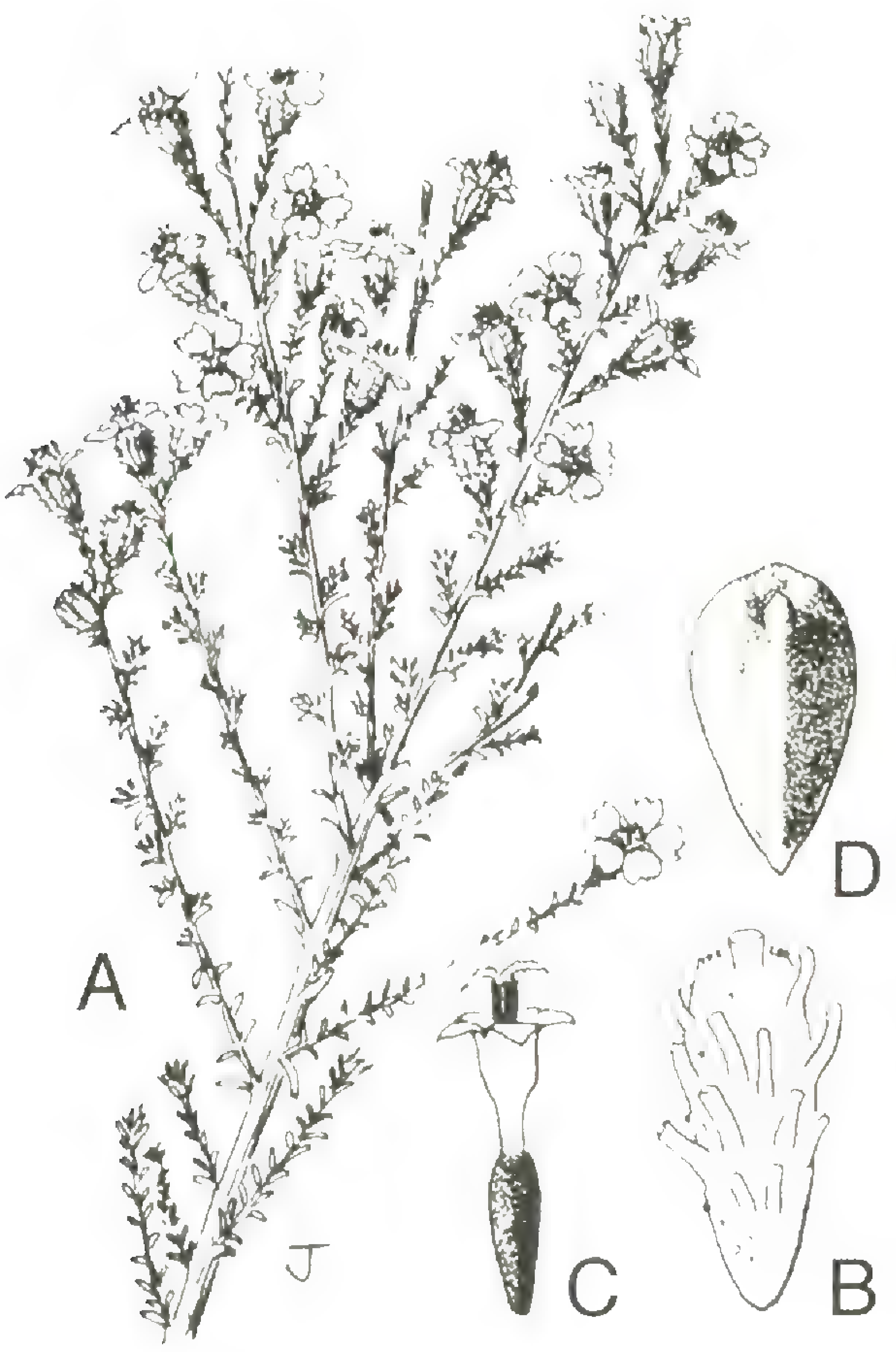
Figure 13. Illustrations of somatic chromosome sets from root-tip preparations for representatives of different populations and species of *Holocarpha* (one chromosome of each pair is shown). Note extensive chromosomal variation among populations of *H. heermannii* and *H. virgata*. Reprinted from *Stages in the Evolution of Plant Species*, by Jens Clausen. Copyright © 1951 by Cornell University. Used by permission of the publisher, Cornell Univ. Press.

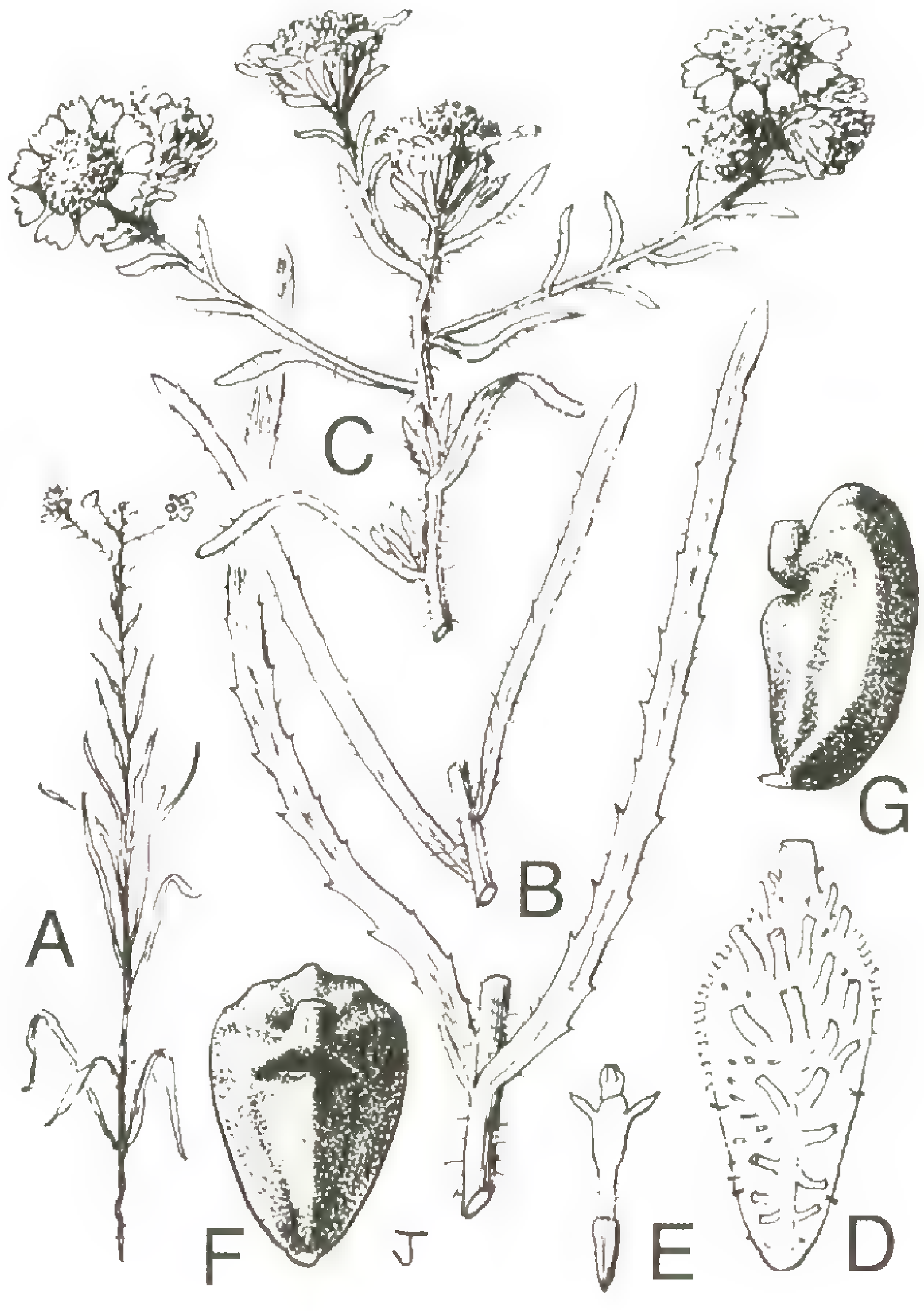
H. macradenia may represent merely "a juvenile form" of the distal-leaf condition in other taxa of *Holocarpha*. Molecular phylogenetic data are most consistent with Palmer's (1987) evolutionary scenario; the actual time of divergence of *H. macradenia* is still under investigation.

As in the origin of *Layia discoidea*, evolutionary divergence of *Holocarpha macradenia* was not accompanied by acquisition of strong internal barriers to gene flow with close relatives; Clausen, Keck, and Hiesey produced a vigorous, partially fertile F_2 generation from crosses between *H. macradenia* and *H. virgata* (Clausen, 1951). Given the great potential for chromosome evolution in *Holocarpha*, the lack of major chromosomal repatterning associated with evolution of the distinctive *H. macradenia* is consistent with the conclusion from studies of *L. discoidea* that genomic reorganization may be less important in rapid evolutionary divergence of peripherally isolated populations than has been widely suggested (see previous section). In contrast, the potential evolutionary importance of ecological selection in the divergence of hypothesized peripheral isolates in both *Layia* and *Holocarpha* is difficult to ignore; climatic and/or edaphic differences between habitats of paraphyletic "progenitor" taxa and nested "derivative" lineages are extreme. In *Holocarpha*, ecological selection also may have played a significant role in maintaining long-term phenotypic stability among morphologically cryptic, intersterile lineages within *H. heermannii* and *H. virgata*; genetic cohesion by gene flow cannot explain morphological stasis in each of the two taxa.

Adaptive Radiation and the "*Madia* Pattern"

Clausen, Keck, and Hiesey's biosystematic investigations in Madiinae led to recognition of extensive intersterility between species then treated as members of *Madia* Molina (Fig. 17). Clausen (1951: 134) stated:





Figures 14 and 15. Ecologically separated, partially interfertile members of *Holocarpha* with four pairs of chromosomes. Figure 14 (left). *Holocarpha virgata*. —A. Capitulescence. —B. Involucral bract (abaxial view). —C. Disk floret. —D. Ray fruit (adaxial view). Figure 15 (right). *Holocarpha macradenia*. —A. Habit. —B. Stem segments. —C. Capitulescence. —D. Involucral bract (abaxial view). —E. Disk floret. —F. Ray fruit (adaxial view). —G. Ray fruit (lateral view).

"The species of *Madia* are cytologically and genetically much more isolated from each other than are the Layias. . . .Most of the species of *Madia* can be linked together through hybrids, but these are sterile, and, moreover, many hybrids have unpaired, nonhomologous chromosomes. There is, therefore, usually only one species to a species complex in *Madia*." In designating five general categories of fertility patterns in vascular plants, Grant (1971: 101) aptly considered "the *Madia* pattern" exemplary of "annual herbs with. . . related species usually separated by incompatibility barriers and by chromosomal and genic sterility barriers." As recognized by Clausen (1951) and Grant (1971), sterility barriers in *Madia* and other plant groups exhibiting the "*Madia* pattern" do not necessarily preclude reticulate evolution; Clausen, Keck, and Hiesey (1945) demonstrated that vigorous, largely sterile hybrids in *Madia* had considerable potential to produce fertile, stable, allopolyploid lineages, such as their synthetic "M. nutrammii" and the wild species, *M. citrigracilis* D. D. Keck.

Subsequent molecular phylogenetic studies of Madiinae and relatives revealed that *Madia*, as treated in all previous senses, was not monophyletic; the smallest clade encompassing all species of *Madia* sensu Clausen (1951; Fig. 18) also included plants that never had been placed in the genus: two perennials from montane California —*Anisocarpus scabridus* (Eastw.) B. G. Baldwin [= *Raillardiopsis scabrida* (Eastw.) Rydb.] (Fig. 19) and *Carlquistia muirii* (A. Gray) B. G. Baldwin [= *Raillardiopsis muirii* (A. Gray) Rydb.] (Fig. 20)—and the endemic Hawaiian silversword alliance, a monophyletic group comprising 30 woody and semi-woody species in *Argyroxiphium* DC., *Dubautia* Gaudich., and *Wilkesia* A. Gray (Baldwin et al., 1991; Baldwin, 1992, 1996, 2003a; Barrier et al., 1999). The two Californian perennials (*A. scabridus* and *C. muirii*) and the silversword alliance were not shown convincingly to be members of Madiinae until publication of Carlquist's (1959b) anatomical investigations, after Clausen, Keck, and Hiesey concluded their experimental studies of the subtribe. Carlquist (1965, 1974, 1980) also championed the hypothesis that the Hawaiian taxa represent a major example of insular adaptive radiation. The silversword alliance includes trees, shrubs, mat-plants, cushion plants, woody vines, and rosette plants, spans most of the wide spectrum of habitats found in the Hawaiian Islands from dry scrub (< 400 mm rainfall/yr) to rainforests and bogs

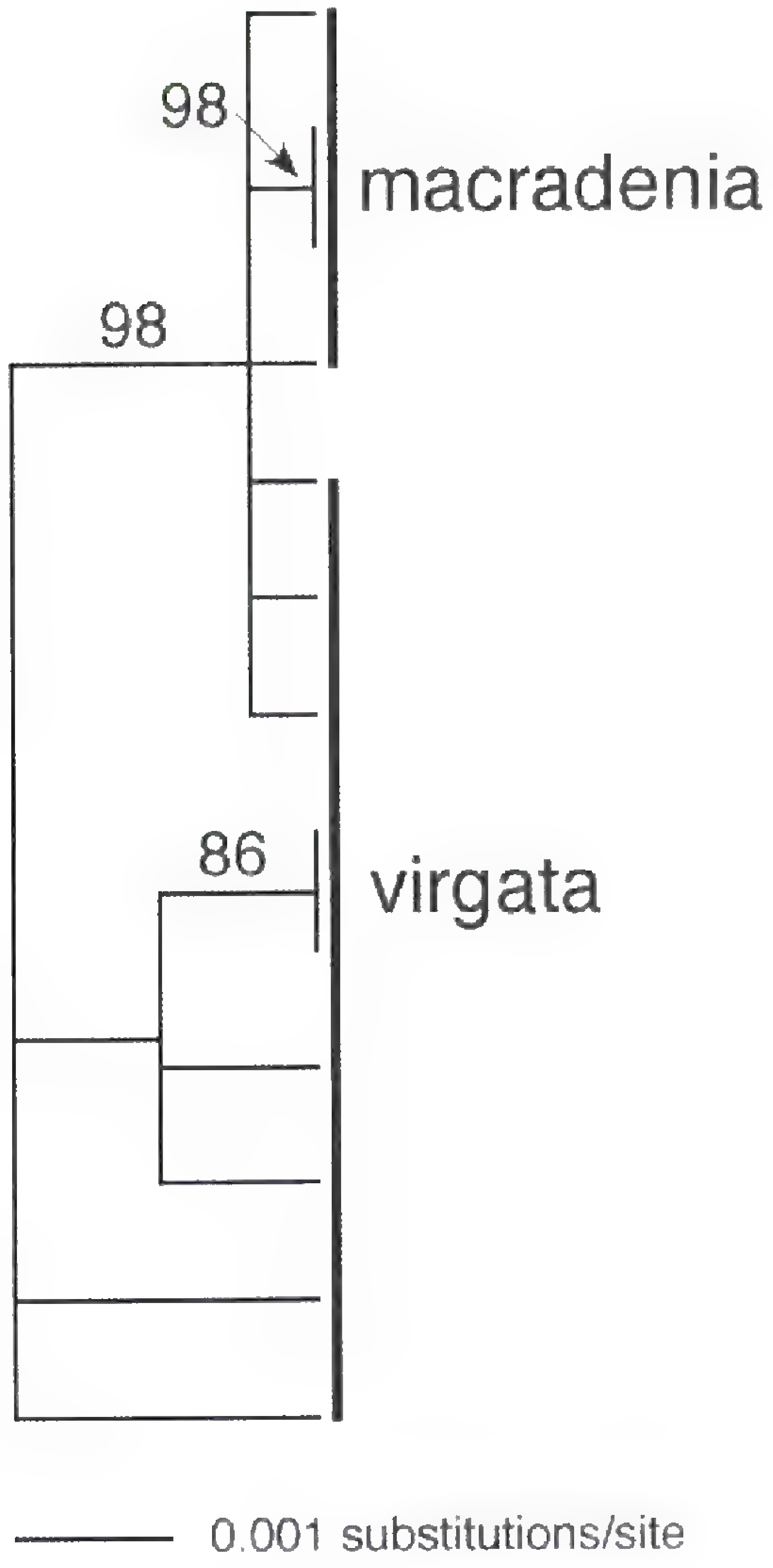


Figure 16. Phylogenetic hypothesis (one of two maximally parsimonious trees) for *Holocarpha macradenia* and *H. virgata* based on analysis of nuclear 18S–26S rDNA external and internal transcribed spacer (ETS and ITS) sequences from representatives of 13 widely-separated populations (Baldwin, unpublished); the clade shown is from a larger tree including representatives of *H. heermannii* and *H. obconica* and outgroup taxa in *Deinandra* [*D. conjugens* (D. D. Keck) B. G. Baldwin and *D. fasciculata* (DC.) Greene]. Branch lengths correspond to relative time since divergence, under maximum-likelihood optimization; rate constancy of ITS evolution across lineages could not be rejected using Felsenstein's (1988) likelihood-ratio test. Numbers along branches are parsimony bootstrap values (only values > 85% are shown).

(> 12,300 mm/yr), and extends along an elevational gradient from near sea level (75 m) to high alpine (3750 m) (Figs. 21–24; Carr, 1985; Carr et al., 1989; Robichaux et al., 1990; Baldwin & Robichaux, 1995; Baldwin, 1997, 2003a, b, c).

Clausen, Keck, and Hiesey were aware of Gray's (1852) early inclusion of the Hawaiian genera *Argyroxiphium* and *Wilkesia* in Madiinae; Keck (1936: 8) conducted a systematic study of *Argyroxiphium* "...with the expectation of treating it in ... Madi(i)nae," and astutely suggested that members of the Hawaiian silversword alliance, as currently recognized, "...would appear to constitute an insular group unto themselves" (Keck, 1936: 10), although his inclusion of *Wilkesia* in *Argyroxiphium* has not been upheld (Carlquist, 1957; Carr & Kyhos, 1986; Baldwin et al., 1990; Baldwin & Robichaux, 1995; Baldwin, 1997). At the same time, Keck rejected Gray's (1852) placement of *Argyroxiphium* and *Wilkesia* in Madiinae and surmised that the silversword alliance was "...probably without close relatives" (Keck, 1936: 10). Keck (1936: 11) concluded: "By thus divorcing *Argyroxiphium* from the American genera to which it has been thought related, the most persistently proposed connection between the ancient element in the Hawaiian flora and the New World has been shattered."

Molecular phylogenetic data on historical ecology and on timing and rate of diversification of the Hawaiian silversword alliance uphold Carlquist's (1965) hypothesis that the Hawaiian taxa represent recent adaptive radiation from a tarweed ancestor rather than an ancient lineage without close relatives, as suggested by Keck (1936). Based on rDNA ITS trees, Osborn's (1902) original, ecological criterion for adaptive radiation is met by the silversword alliance; major ecological shifts between wet and dry habitats were evidently associated with diversification on each of the four major island groups occupied by the lineage, with the possible exception of the youngest island, Hawai'i (Fig. 25; Baldwin & Robichaux, 1995; see also Robichaux et al., 1990). Simpson's (1944) rapid-diversification criterion for adaptive radiation is also met; inability to reject rate constancy of molecular evolution across clades in the ITS trees and time-calibration of a node outside the Hawaiian lineage allowed estimation of a maximum age for the most recent common ancestor of the silversword alliance at 5.2 ± 0.8 million years and a minimum diversification rate for the group of 0.56 ± 0.17 species per million years (Fig. 26; Baldwin & Sanderson, 1998). The estimated maximum age of the silversword alliance is roughly comparable to the age of the oldest modern high-island, Kaua'i (ca. 5.1 million years; Clague & Dalrymple, 1987) and much younger than the > 10 million-year-old estimated ages of some other prominent examples of adaptive radiation in the Hawaiian Islands, such as Hawaiian drosophilids (Thomas & Hunt, 1991) and Hawaiian lobelioids (Givnish et al., 1996). The minimum diversification rate estimated for the silversword alliance falls within the upper range of estimated rates for various continental radiations of plants and animals and was regarded by Nee (2001: 661) as "remarkably high."

An expanded perspective on *Madia* that encompasses all of the "Madia" lineage (Baldwin, 1996; Fig. 18), i.e., the clade including all of the taxa in

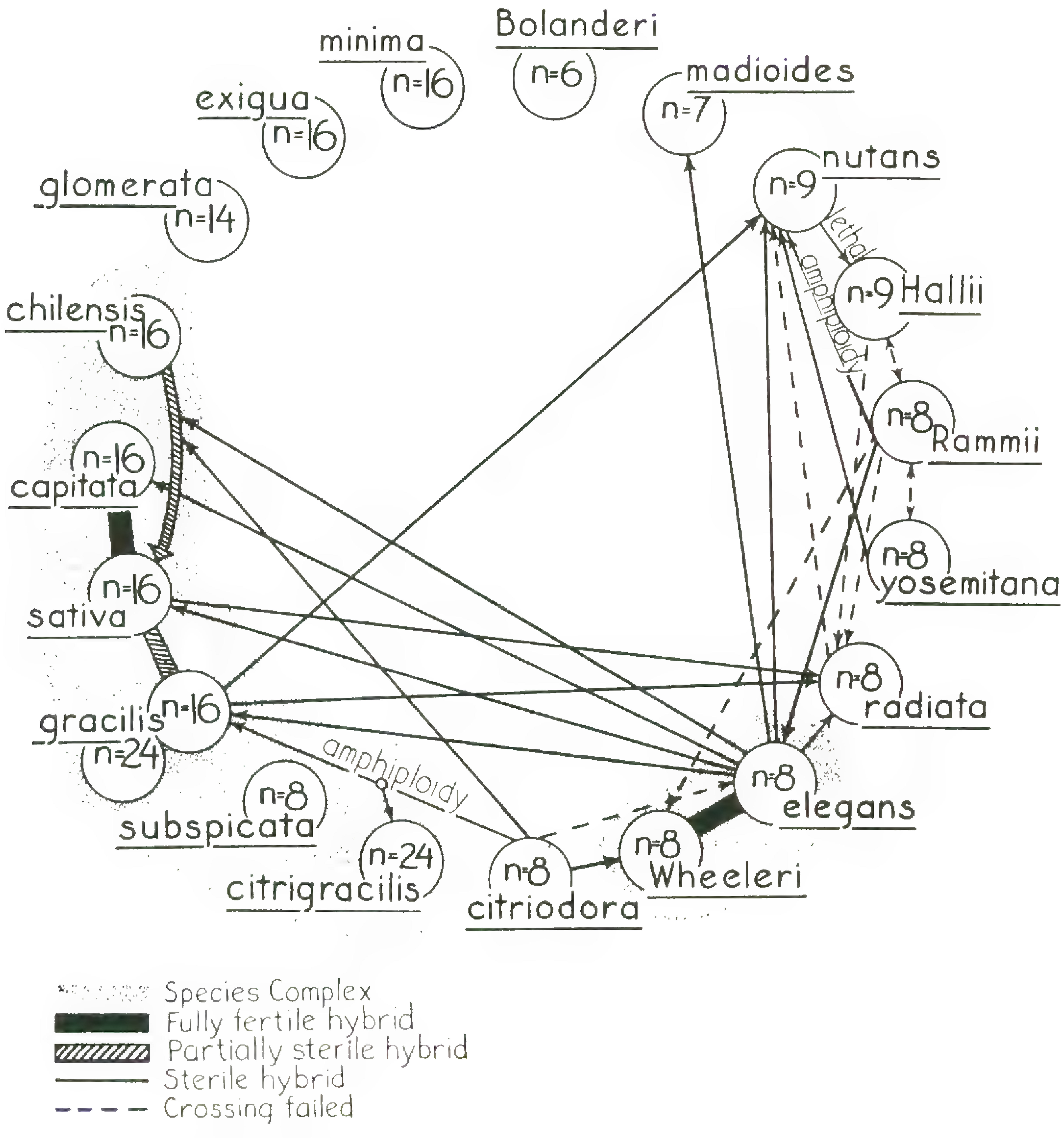


Figure 17. Crossing diagram of *Madia* sensu Clausen (1951). Fully interfertile taxa shown in the diagram are now treated as taxonomically indistinct (*Madia capitata* Nutt. and *M. chilensis* (Nutt.) Reiche are now treated as synonyms of *M. sativa* Molina; *Madia wheeleri* (A. Gray) D. D. Keck is now treated as a synonym of *M. elegans* D. Don ex Lindl.). Some species are now treated in other genera, i.e., *Anisocarpus* Nutt. [*A. madioides* Nutt.], *Harmonia* B. G. Baldwin [*H. hallii* (D. D. Keck) B. G. Baldwin, *H. nutans* (Greene) B. G. Baldwin], *Hemizonella* (A. Gray) A. Gray [*H. minima* (A. Gray) A. Gray], *Jensia* B. G. Baldwin [*J. rammii* (Greene) B. G. Baldwin, *J. yosemitana* (Parry ex A. Gray) B. G. Baldwin], and *Kyhosia* B. G. Baldwin [*K. bolanderi* (A. Gray) B. G. Baldwin]. All taxa shown are annuals except for *Anisocarpus madioides* and *Kyhosia bolanderi*, which are perennial herbs. The "Madia" lineage (Baldwin, 1996) also includes *Anisocarpus scabridus*, *Carlquistia muirii*, and the Hawaiian silversword alliance (30 species in *Argyroxiphium*, *Dubautia*, and *Wilkesia*). Reprinted from *Stages in the Evolution of Plant Species*, by Jens Clausen. Copyright © 1951 by Cornell University. Used by permission of the publisher, Cornell University Press.

Madia sensu Clausen, Keck, and Hiesey (Fig. 17) plus *Anisocarpus scabridus*, *Carlquistia muirii*, and the Hawaiian silversword alliance, reveals strongly contrasting patterns of phenotypic divergence. Life-form evolution and habitat shifts among continental members of the "Madia" lineage (and among continental tarweeds in general) are dwarfed by adaptive radiation of the Hawaiian silversword alliance: the continental taxa of the group are annual and perennial herbs that occur along a relatively narrow precipitation gradient compared to the wide range of dry, wet, and boggy situations occupied by the semi-woody and

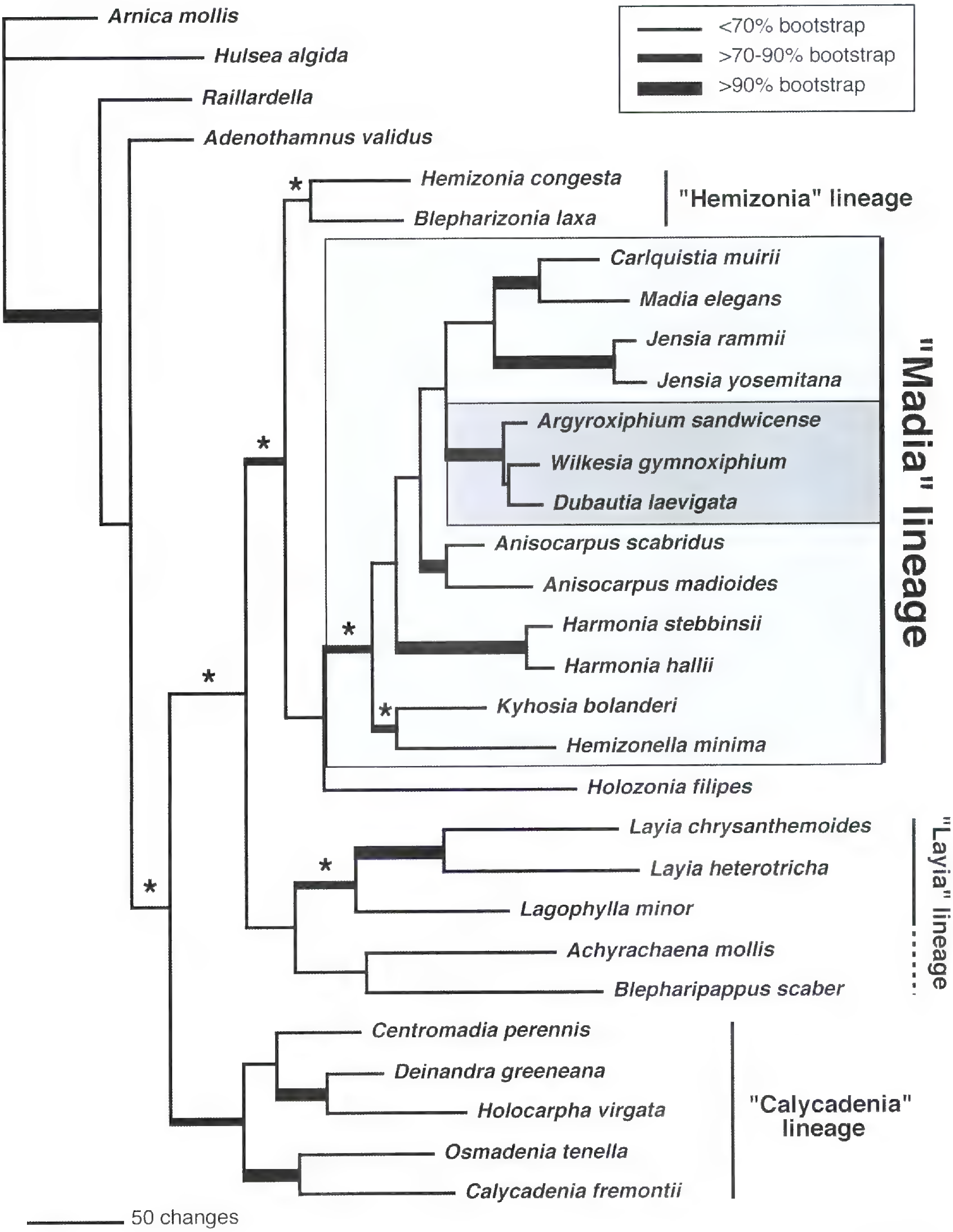
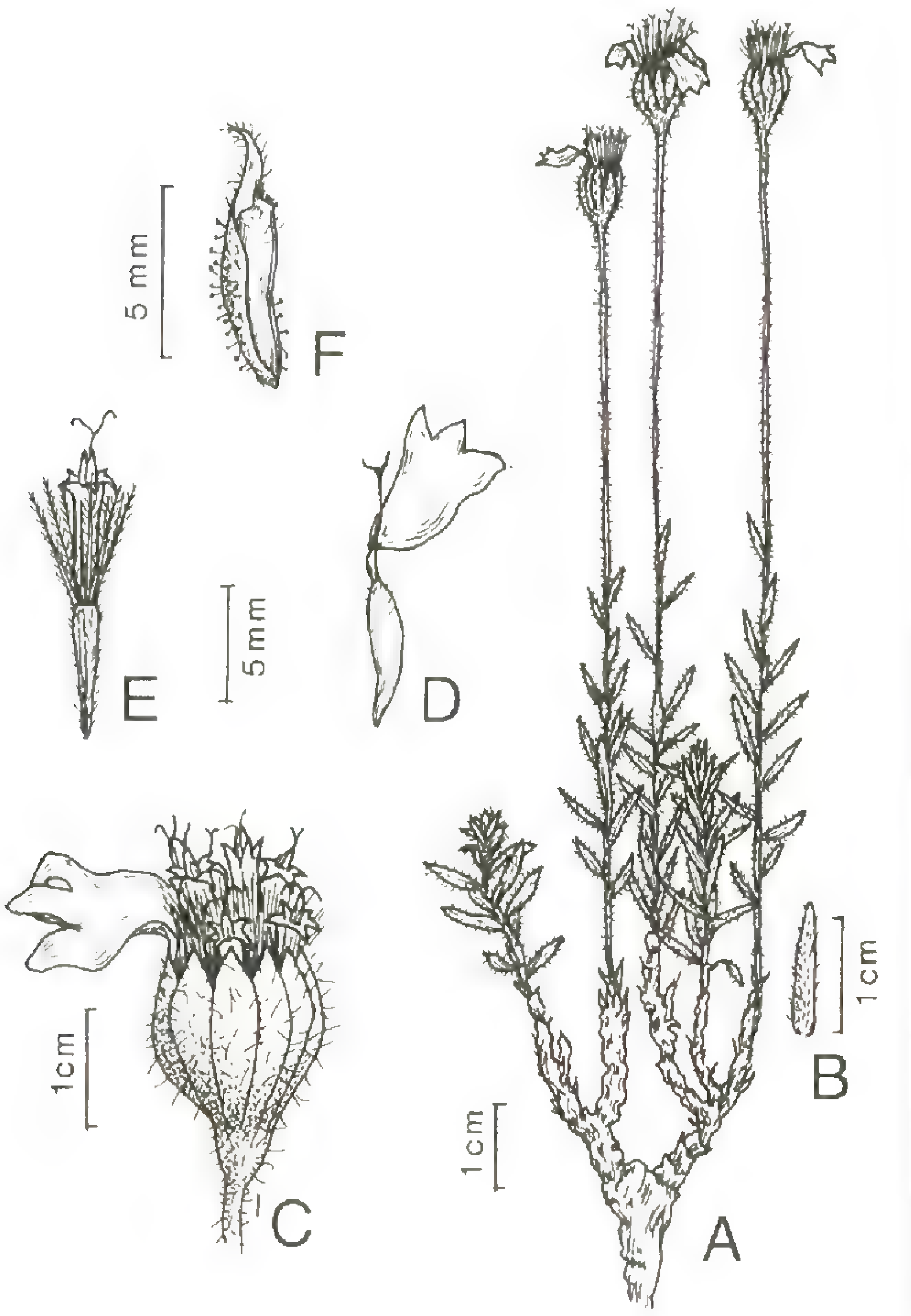
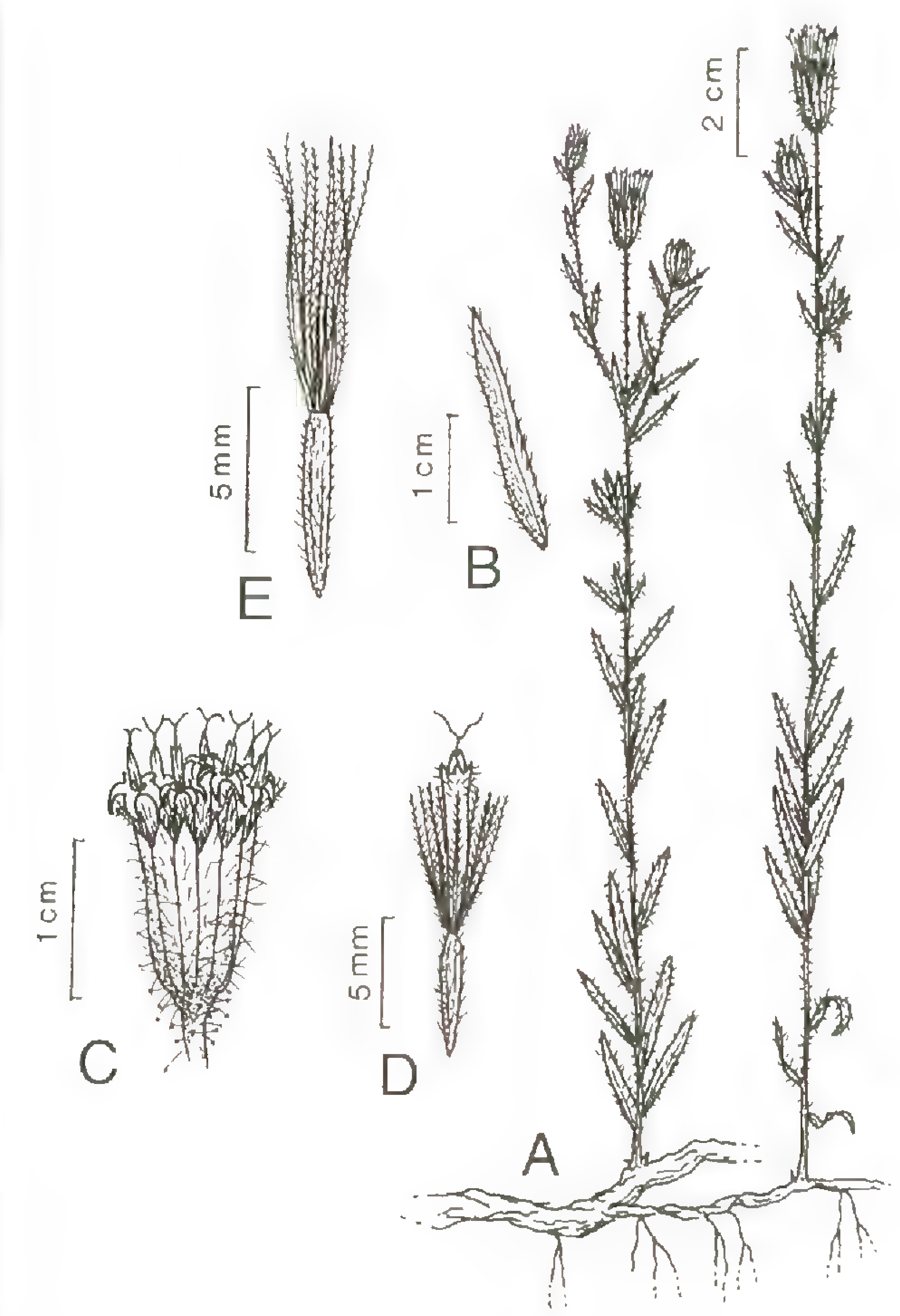


Figure 18. Phylogenetic hypothesis (the most parsimonious tree) for Madiinae based on simultaneous analysis of chloroplast DNA (*trn*K intron) and 18S–26S nuclear ribosomal DNA external and internal transcribed spacer (ETS and ITS) sequences (Baldwin, 2003a, unpublished). The dark box nested within the "Madia" lineage encloses the clade corresponding to the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*). Asterisks (*) indicate that branch support rises to the next level indicated by branch widths with removal of sequences for the three long-branch, monotypic genera: *Achyrachaena* Schauer, *Blepharipappus* Hook., and *Holozonia* Greene. *Raillardella* (A. Gray) Benth. is represented by a *trn*K intron sequence of *R. argentea* (A. Gray) A. Gray and ETS and ITS sequences of *R. pringlei*. Allopolyploidy of the Hawaiian silversword alliance (Barrier et al., 1999) is not resolved by chloroplast DNA or nuclear rDNA sequences. See Appendix 1 for authorship of species names not mentioned in text.





Figures 19 and 20. Californian montane perennials of the "Madia" lineage, not included in *Madia* sensu Clausen (1951); although both diploid species were previously treated in *Raillardiopsis* Rydb., the genome of each is evidently more closely related to a different genome in the (allotetraploid) Hawaiian silversword alliance than to the genome in the other diploid (Barrier et al., 1999). Figure 19 (left). *Anisocarpus scabridus.* A. Habit. —B. Leaf. —C. Head. —D. Ray floret. —E. Disk floret. —F. Ray fruit and half-enveloping involucral bract (obliquely adaxial view). Figure 20 (right). *Carlquistia muirii.* —A. Habit. —B. Leaf. —C. Head. —D. Floret. —E. Fruit with pappus. Both species have been involved in successful crosses with one another and with members of the Hawaiian silversword alliance (Baldwin et al., 1991; Carr et al., 1996; Barrier et al., 1999).

woody Hawaiian species (see Baldwin, 2003a, b, c). Phylogenetic evidence for origin of the silversword alliance after considerable diversification of the "Madia" lineage (Figs. 18, 26; see also Barrier et al., 1999) indicates that ecological diversity in the Hawaiian lineage represents a major acceleration of evolutionary change associated with colonization of the Hawaiian Islands. As suggested for diverse oceanic-island lineages in general, adaptive radiation of the silversword alliance probably has been in large part a consequence of ecological opportunity (Simpson, 1953; see Schluter, 2000), with availability of a wide array of empty niches in the Hawaiian Islands and lack of interference with other organisms, possibly aided by intrinsic factors promoting evolutionary change, such as the allopolyploid constitution of the group (Barrier et al., 1999).

Extension of Clausen's (1951) crossing results to encompass perennial members of the "Madia" lineage has indicated strikingly different fertility patterns between the continental and Hawaiian taxa. Crosses between the continental perennials and between the continental and Hawaiian perennials of the "Madia" lineage, not attempted by Clausen, Keck, and Hiesey (see Fig. 17), either have failed or yielded vigorous F_1 hybrids of extremely low pollen stainability (an estimate of fertility), with most stainable grains being abnormally large, tetraporate, and putatively diploid (Kyhos et al., 1990; Baldwin et al., 1991; Carr et al., 1996; Barrier et al., 1999). Observed lack of interfertility between the continental perennials and between the continental and Hawaiian perennials conforms to the results obtained by Clausen, Keck, and Hiesey for the annual members of the lineage (Clausen, 1951) and to the "*Madia* pattern" described by Grant (1971). In contrast, crosses between members of the Hawaiian silversword alliance have yielded vigorous, partially to fully fertile hybrids in all interspecific and intergeneric combinations attempted, despite major morphological and ecological divergence of the taxa (Fig. 27; Carr & Kyhos, 1981, 1986; Carr, 1985, 2003a). Reduced fertility in some Hawaiian hybrid combinations can be attributed

Figures 21–21. Members of the Hawaiian silversword alliance. Figure 21 (upper left). *Argyroxiphium sandwicense* DC. subsp. *macrocephalum* (A. Gray) Meyrat, a monocarpic, thick-leaved rosette plant of dry, alpine, cinder slopes and flats on Haleakala, East Maui. —A. Habit. —B. Head. Figure 22 (upper right). *Dubautia latifolia* (A. Gray) D. D. Keck, a liana (woody climber) of mesic to wet forests on Kaua'i. Figure 23 (lower left). *Dubautia reticulata* (Sherff) D. D. Keck, a tree or large shrub of wet forests on East Maui. Figure 24 (lower right). *Wilkesia gymnoxiphium* A. Gray, a monocarpic, fibrous-leaved rosette plant of dry slopes and ridges on Kaua'i. —A. Habit. —B. Segment of capitulescence. —C. Head and distal peduncle.

mostly or solely to one to three whole-arm reciprocal translocations that differentiate genomes of the group (Carr & Kyhos, 1986; Carr, 2003b). Even hybrids of low fertility, i.e., between *Argyroxiphium sandwicense* DC. subsp. *macrocephalum* (A. Gray) Meyrat and *Dubautia menziesii* (A. Gray) D. D. Keck, have been shown to serve as effective pollen parents in backcrosses, with recovery of full fertility in a subset of B_2 progeny (Carr, 1995, 2003a). Ecological (post-dispersal) selection against hybrids appears to be important in limiting gene flow in the Hawaiian group (Carr, 1995), although such selection has not pre-

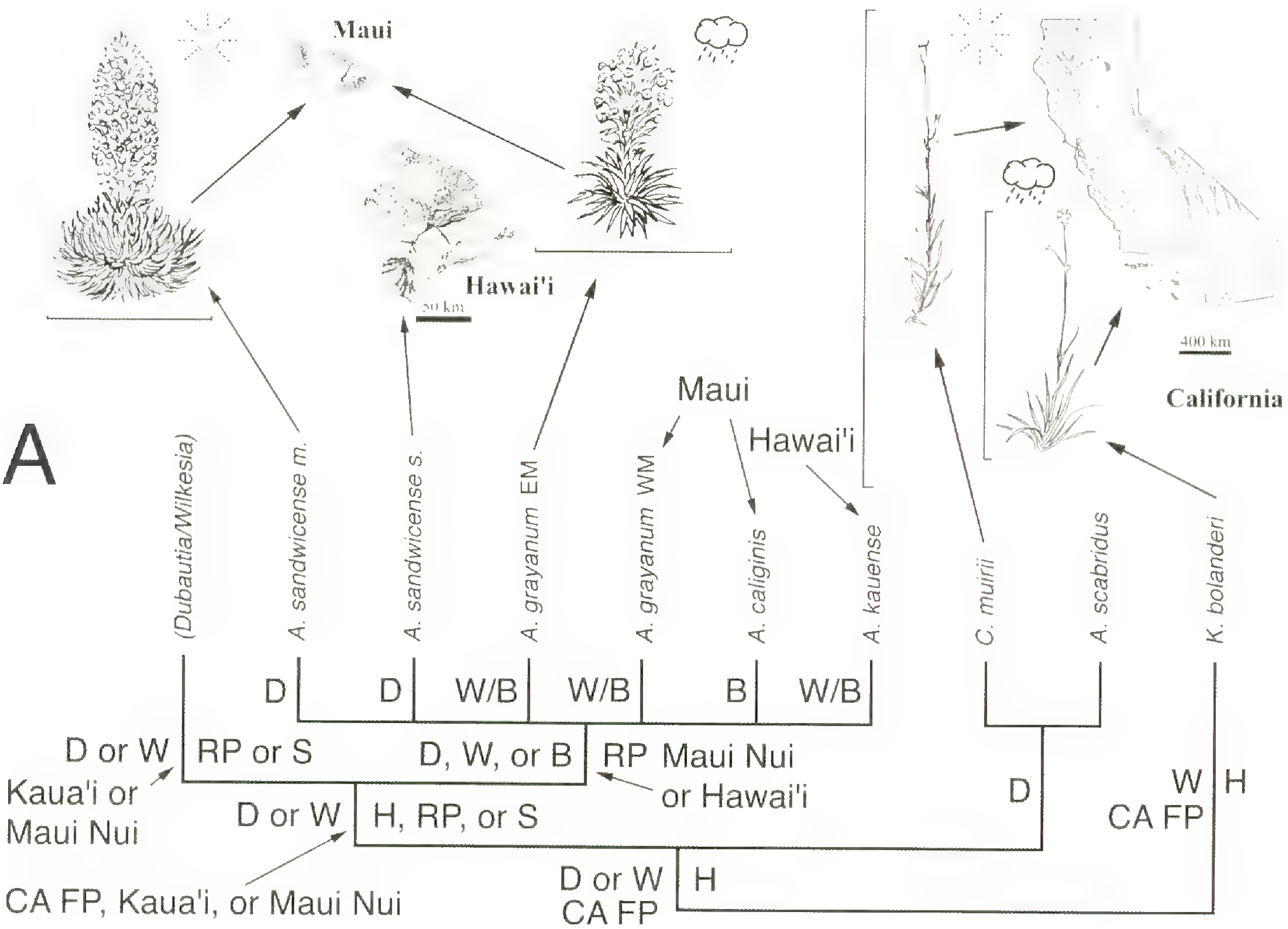
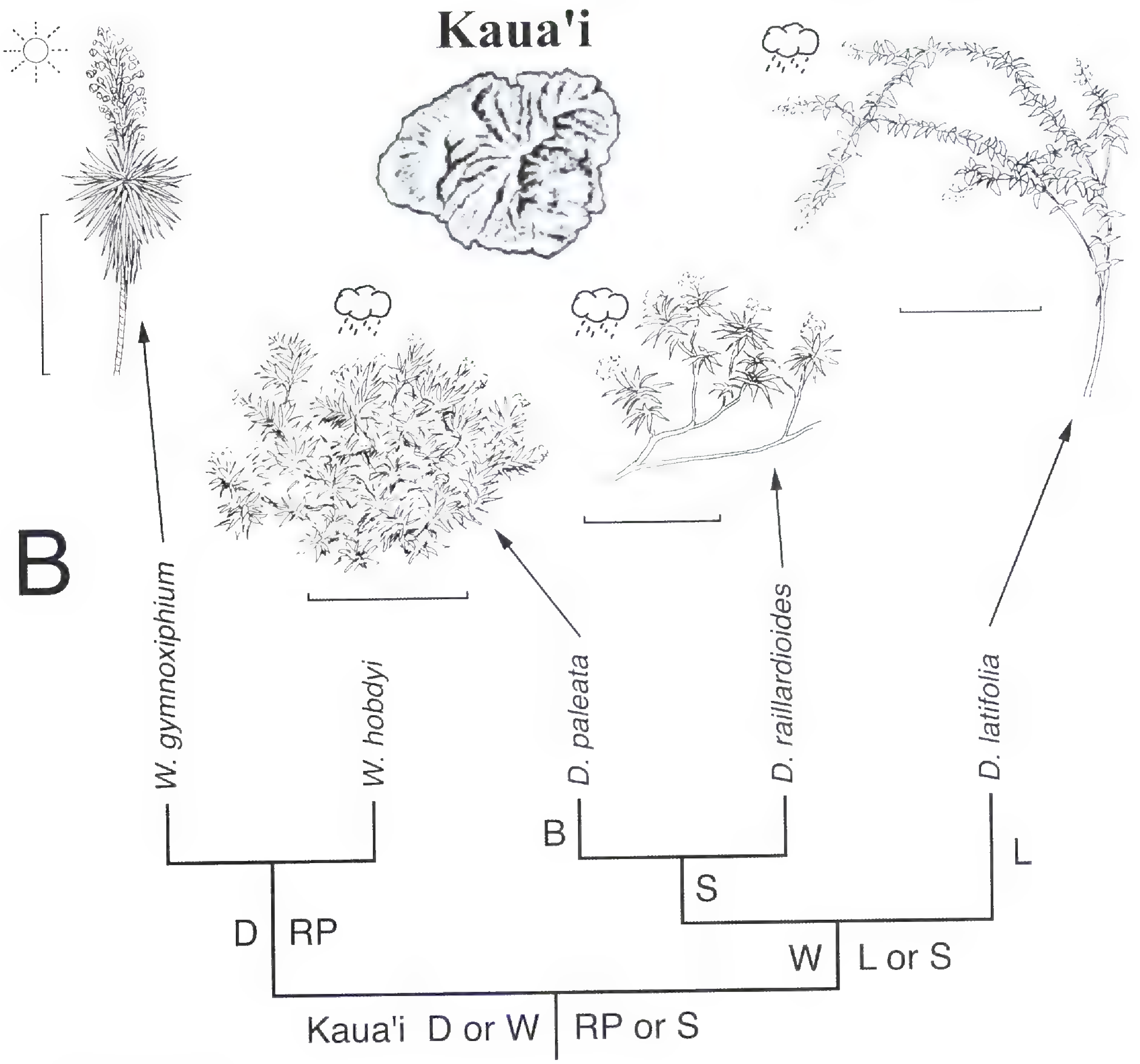


Figure 25 (pp. 84–87). Ecological shifts and major dispersal events during diversification of each of four principal lineages of the Hawaiian silversword alliance, based on the semi-strict consensus of eight maximally parsimonious nuclear rDNA ITS trees (reprinted or adapted from Baldwin, 1997; data from Baldwin & Robichaux, 1995). —A. *Argyroxiphium*, a young-island group (Maui and Hawai'i), shown in context of "*Dubautia/Wilkesia*" lineage (detailed in Figs. 25B, C, and D) and western North American outgroup taxa— montane, perennial tarweeds of the "Madia" lineage (in *Anisocarpus*, *Carlquistia*, and *Kyhosia*). —B. *Wilkesia* and sister group (part of *Dubautia*), restricted to Kaua'i. Habitat abbreviations and symbols: B = bog; D or sun symbol = dry; W = wet; cloud symbol = wet or bog. Habit symbols: H = herb; L = liana (woody climber); M = mat-plant; RP = rosette plant (monocarpic or polycarpic); S = shrub; T = tree. Geographic key: CA FP = California Floristic Province; Maui Nui = prehistoric island uniting Lana'i, Moloka'i, and Maui (and Kaho'olawe, where no members of Madiinae are known to occur). Placement of geographic area, habitat, and habit along branches is where ancestral state is unequivocal based on parsimony criterion (Baldwin & Robichaux, 1995). Island occurrences and life-form information for the silversword alliance conform with Carr (1985, 1999). Taxonomic abbreviations: *A. sandwicense*— "*m.*" = subsp. *macrocephalum*, "*s.*" = subsp. *sandwicense*; *D. ciliolata* (DC.) D. D. Keck — "*c.*" = subsp. *ciliolata*, "*g.*" = subsp. *glutinosa* G. D. Carr; *D. knudsenii* Hillebr.— "*f.*" = subsp. *filiformis* G. D. Carr, "*k.*" = subsp. *knudsenii*, "*n.*" = subsp. *nagatae* (H. St. John) G. D. Carr; *D. laxa* Hook. & Arn. — "*h.*" = subsp. *hirsuta* (Hillebr.) G. D. Carr, "*l.*" = subsp. *laxa*; *D. linearis* (Gaudich.) D. D. Keck— "*h.*" = subsp. *hillebrandii* (H. Mann) G. D. Carr, "*l.*" = subsp. *linearis*; *D. plantaginea* Gaudich. — "BH" ("Blue Hole") = subsp. *magnifolia* (Sherff.) G. D. Carr, "*h.*" = subsp. *humilis* G. D. Carr, "*p.*" = subsp. *plantaginea*; *D. scabra* (DC.) D. D. Keck— "*l.*" = subsp. *leiophylla* (A. Gray) G. D. Carr, "*s.*" = subsp. *scabra*. See Appendix 1 for authorship of species names not mentioned in text.

cluded establishment of hybrids; 38 naturally occurring hybrid combinations between different pairs of species (including intergeneric hybrids) have been documented by Carr (2003a), and evidence for both recent and ancient introgression has been obtained from studies of hybrid zones (Crins et al., 1988; Caraway et al., 2001) and comparison of phylogenetic data from cytogenetic, nuclear rDNA, and chloroplast DNA studies (Baldwin et al., 1990; Baldwin, 1997, 2003c). Hybrid speciation, as well, may explain some conflicts between different lines of phylogenetic data, e.g., for *D. scabra* (DC.) D. D. Keck (Baldwin et al., 1990; Baldwin, 1997).

The stark contrast between the Hawaiian pattern of interfertility across phenotypically disparate lineages and the pattern of intersterility seen across the less distinctive continental species of the "Madia" lineage has evolutionary implications. Lack of strong, intrinsic reproductive barriers between species and genera of the Hawaiian silversword alliance leaves open the potential for homoploid hybrid speciation or introgression involving plants that differ greatly in



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life-form or ecological setting, particularly under environmental conditions favorable to recombinant phenotypes (Carr, 1995, 2003a). Intersterility barriers among continental species of the "Madia" lineage may limit the evolutionary potential of hybridization to formation of allopolyploids, as demonstrated experimentally by Clausen et al. (1945) for some annual species and as meiotic behavior and diploid pollen formation indicate for hybrids between the continental perennials (Carr et al., 1996; Barrier et al., 1999). Such allopolyploidy has contributed only modestly to diversity in the continental lineages (e.g., *Madia citrigracilis*), but evidently gave rise to the lineage that successfully colonized the Hawaiian Islands and became the silversword alliance (Barrier et al., 1999).

Phylogenetic data from ITS sequences on time since divergence of perennials in the "Madia" lineage (Baldwin & Sanderson, 1998) allows patterns of interfertility to be placed in an understandable perspective (Fig. 26). Lack of interfertility between continental perennials and between continental and Hawaiian perennials may be explained simply by the longer timeframe for evolutionary divergence between those lineages compared to the time since divergence of the Hawaiian lineages from a common ancestor, with gradual breakdown in interfertility through time as a by-product of divergence. Interfertility between members of the silversword alliance is consistent with fertility patterns seen in other (mostly perennial) lineages of Hawaiian angiosperms (see Carr, 1998; Baldwin, 1998) and conforms more closely to the common fertility pattern seen in young woody plant groups in general, i.e., the "*Ceanothus* pattern" (Grant, 1971), than to the "*Madia* pattern," seen widely in annuals (Grant, 1971). Although the relative

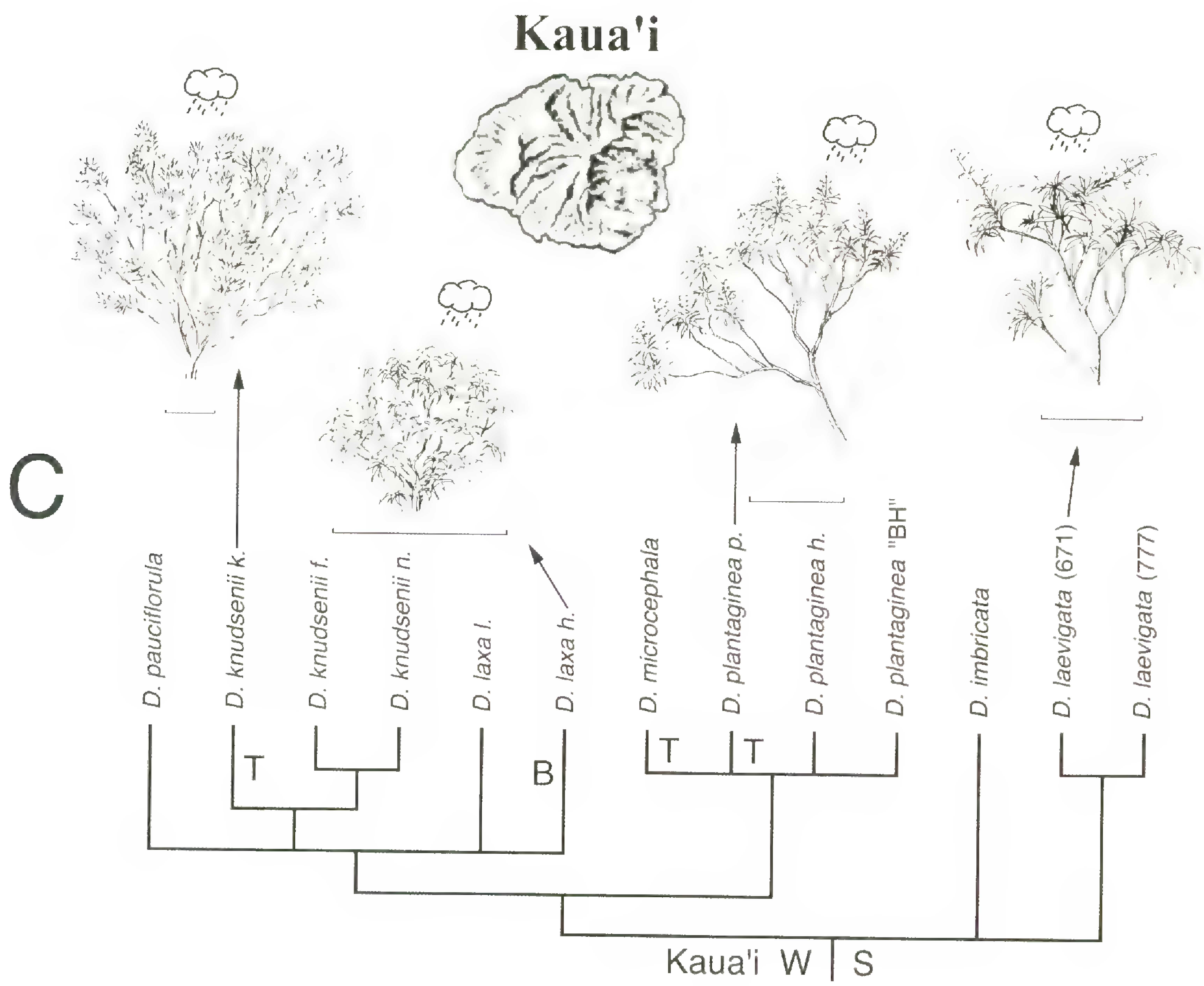

Figure 25. Continued. —C. Members of *Dubautia* with genomic arrangements DG1 and DG3 (Carr & Kyhos, 1986, pers. comm.), native (but not all endemic) to Kaua'i. —D. *Dubautia* sect. *Railliardia*, restricted to one or more young island(s) (not on Kaua'i). For additional details, see p. 84.

timing of divergence of annuals and perennials in the "Madia lineage" has not yet been resolved, the generally higher rates of rDNA evolution in the annuals compared to the perennials (Baldwin & Sanderson, 1998) accords with findings for some other angiosperms (e.g., *Sidalcea* A. Gray; Andreasen & Baldwin, 2001) and may reflect more general rates of molecular evolution, which, in turn, could bear on a putatively higher rate of acquisition of post-zygotic reproductive barriers between annuals than between perennials in general. Similar results have been obtained in comparisons between phylogenetic and crossing data for continental annual and insular perennial lineages of the tarweed genus *Deinandra* Greene (Baldwin, unpublished). These findings reinforce Grant's (1971) observations on associations among life history, patterns of interfertility, and the evolutionary potential of hybridization in plants, and illustrate further contrasts in patterns and processes of evolutionary change among closely related lineages of Madiinae.

Conclusions

Evolutionary investigations of Madiinae in the wake of Clausen, Keck, and Hiesey's pioneering research have led to a greatly expanded circumscription of the subtribe and a more detailed understanding of processes and patterns of diversification in the group. Progress in resolving evolutionary questions in Madiinae through integration of diverse lines of evidence follows in the tradition of Clausen, Keck, and Hiesey and reaffirms the value of systematic data for tackling process-oriented evolutionary questions, as appreciated by the Carnegie team. Clausen, Keck, and Hiesey's evidence for a dynamic evolutionary history of Madiinae, both in relative rates of morphological, ecological, and genetic change and in modes of diversification, has been upheld and extended to finer-scale levels than in the comparisons among genera described by Clausen (1951). Even within individual genera of Madiinae, processes of evolutionary change and the biological properties of

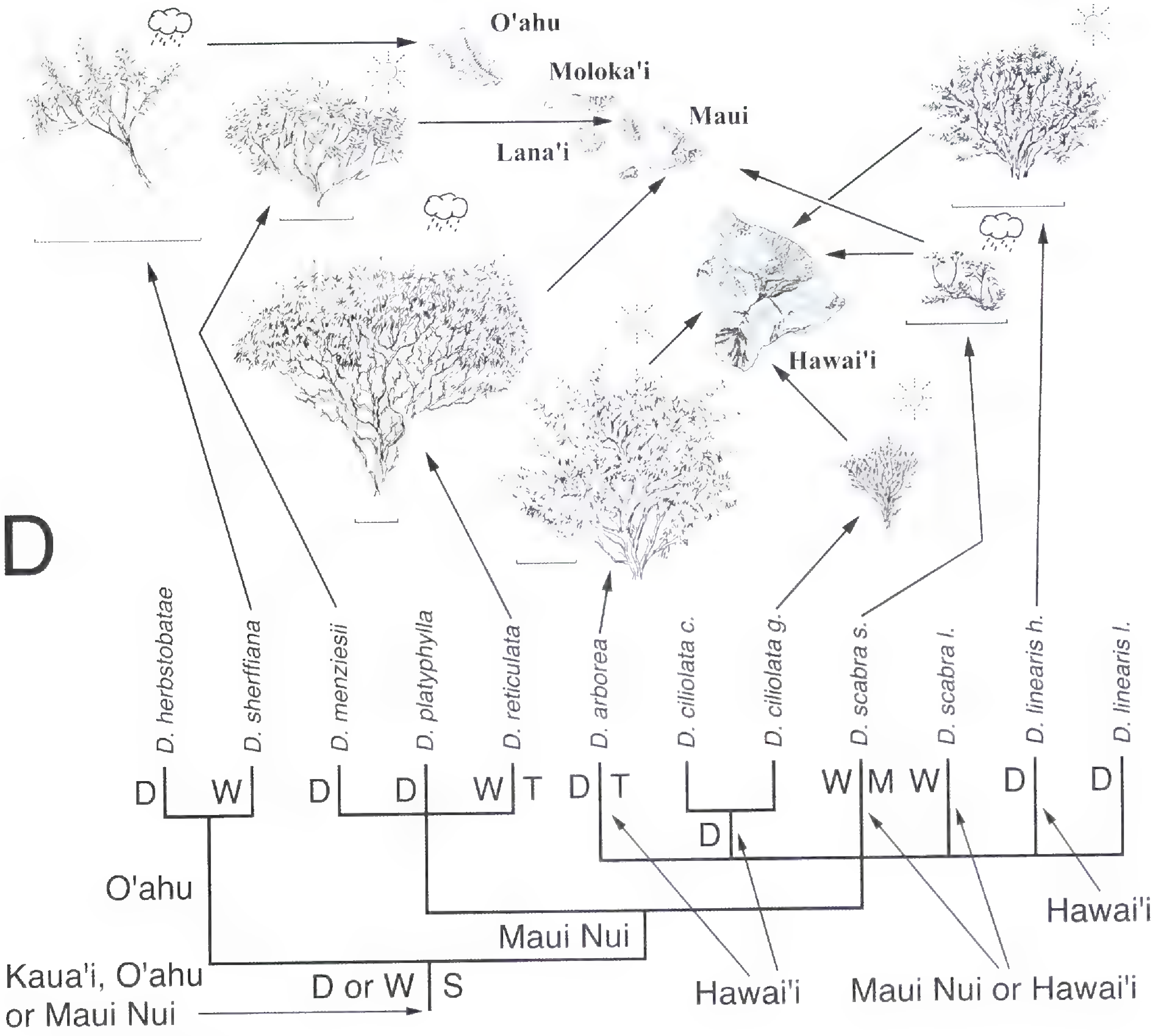

Figure 25. Continued.

lineages may differ greatly. These results underscore the value of phylogenetic data in process-oriented evolutionary studies and the importance of phylogenetic considerations in classification at all levels of evolutionary divergence.

A recurring finding in the re-examination of tarweed evolution using modern systematic approaches has been the discovery of cryptic or semicryptic diversity, even in groups that were studied intensively by Clausen, Keck, and Hiesey from an experimental biosystematic perspective (e.g., *Layia*). In part, such diversity appears to reflect ecologically differentiated and evolutionarily divergent—though often interfertile—lineages, as in *L. gaillardioides*. Similar examples have emerged recently from molecular phylogenetic and ecological studies of other plant taxa that were a focus of previous experimental work, such as *Lasthenia* Cass. (Ornduff, 1966; Chan et al., 2002; Rajakaruna et al., 2003). The potential importance of ecologically distinct, cryptic groups was well appreciated by Clausen (1951: 29–30): "It is now established as a general biological law that species that occupy many kinds of environment are able to do so because they have evolved series of physiologically distinct races, each of which survives within its native zone but is less able to compete in neighboring zones and usually is unable to survive in the extreme ranges of the species. This fitness is primarily physiological; it is determined by genes, and it may or may not be expressed in the external appearance of the plant. Ecological races or ecotypes have therefore generally been overlooked by taxonomists, geneticists, and ecologists, all of whom looked for visible characters that they could classify. Actually, however, the ecological race is a far more important biological entity than the morphological subspecies." Although infeasible during Clausen's life, resolving "ecological races" that correspond to natural groups worthy of taxonomic recognition is now possible and desirable, especially in light of the

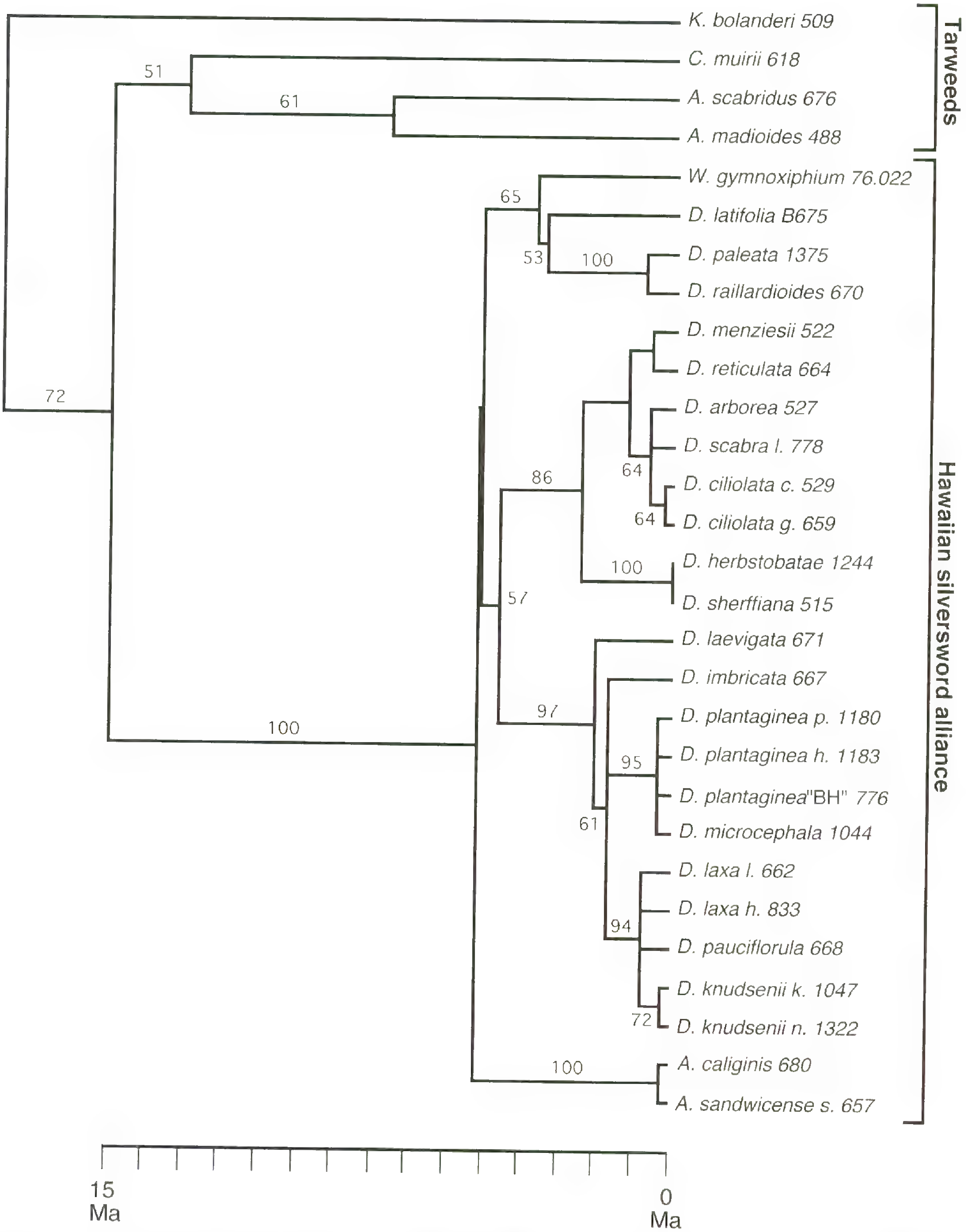

Figure 26. A phylogenetic hypothesis (one of four maximally parsimonious trees) for perennial members of the "Madia" lineage, with time-calibrated branches, based on nuclear rDNA ITS sequences (adapted from Baldwin & Sanderson, 1998). Continental tarweeds (*Anisocarpus*, *Carlquistia* B. G. Baldwin, and *Kyhosia*) and the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*) were included in the analysis. The outgroup (*Adenothamnus validus* and *Raillardella pringlei*) is not shown. Rate-constancy of molecular evolution across lineages could not be rejected using Felsenstein's (1988) likelihood-ratio test; branch lengths were optimized to conform to clock-like evolution using maximum likelihood. External calibration of the node representing the most recent common ancestor of the continental perennials and the Hawaiian taxa was based on the assumption that diversification above that node would not have occurred until after mid-Miocene (15 million years ago), when summer precipitation in western North America began to decline (nearly all continental tarweeds are restricted to areas of summer-dry climate; see Baldwin & Sanderson, 1998). See Figure 25 caption for abbreviations of subspecies in *Dubautia*.

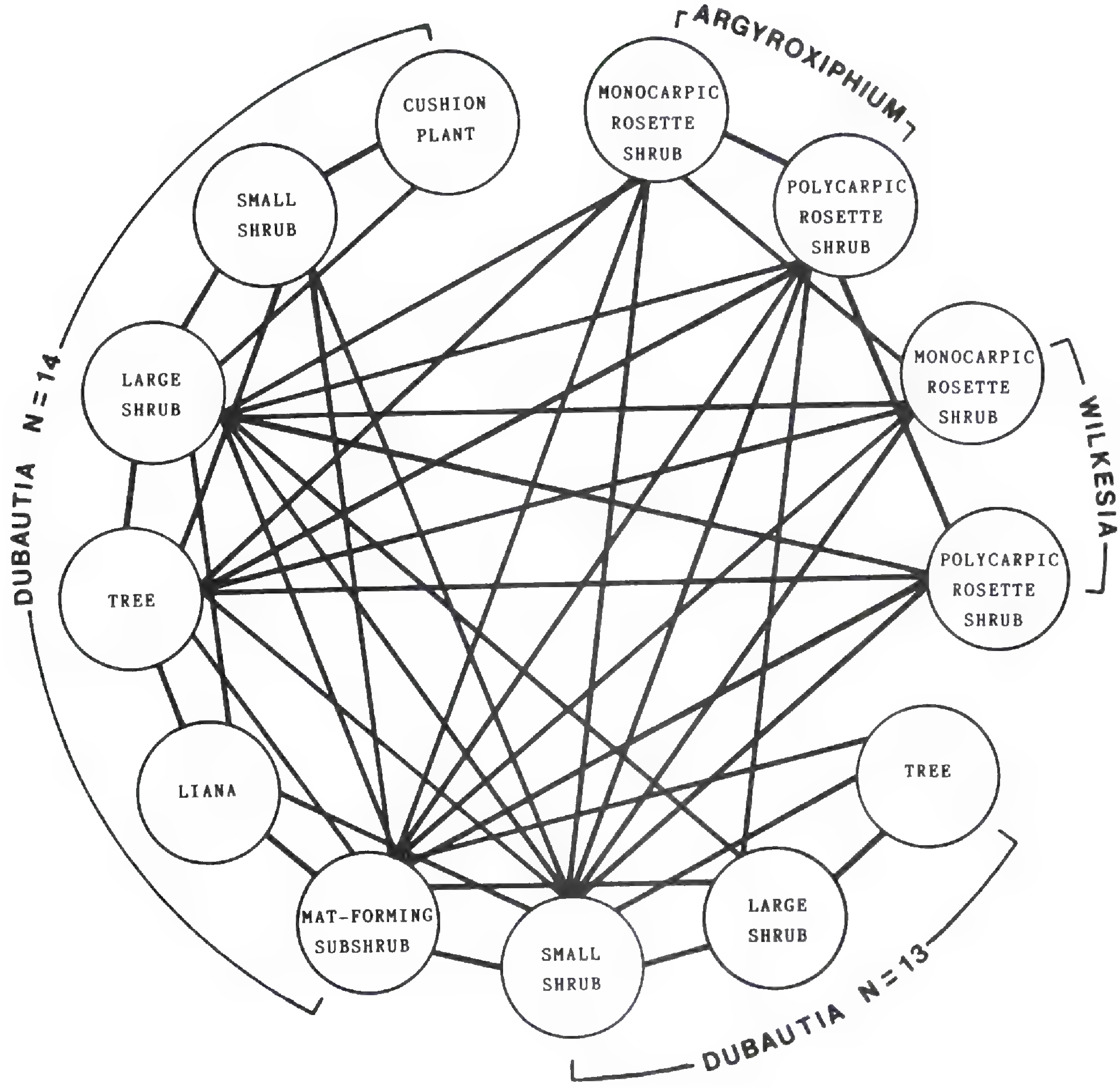

Figure 27. Crossing diagram showing synthetic and natural hybrids between species of different life-form in the Hawaiian silversword alliance based on data of Carr (1985) and Carr and Kyhos (1981, 1986). Crosses in all attempted combinations were successful and yielded hybrids of at least partial fertility. Reprinted from Carr et al. (1989) with permission of the publisher, Oxford University Press.

potential evolutionary importance of such lineages in the face of rapid global change. An important challenge in the coming years for systematists working in well-studied, threatened floras, such as the California flora, will be to resolve ecologically significant, overlooked diversity through application of molecular phylogenetic and experimental approaches, much in the spirit of Clausen, Keck, and Hiesey's classic investigations (see Baldwin, 2000).

The potential of modern plant systematics to contribute to understanding of evolutionary processes and fine-scale diversity is just beginning to be realized, with exciting results (e.g., Rieseberg, 2006 this volume; Sakai et al., 2006 this volume). Spectacular progress by systematists in resolving higher-level plant relationships through application of molecular phylogenetic methods has created an invaluable framework for integrative systematic studies of young lineages. Recent methodological advances in systematics that allow rigorous estimation of divergence times and diversification rates and the explosive growth in comparative methods have much potential to aid systematists in taking phylogenetic hypotheses beyond the limitations of strictly pattern-based considerations and toward better informed conclusions about how and why evolutionary changes have occurred. The promise of collaborative studies of plant diversification that bring together the combined strengths of systematists, ecologists, and geneticists, so well demonstrated by Clausen, Keck, and Hiesey, has never been greater.

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APPENDIX 1. Authorities for species presented in the figures when otherwise not provided in the text. For a complete listing of accepted names and synonyms for specific and infraspecific taxa in Madiniiae, see Carr et al., 2003.

Achyrachaena mollis Schauer
Argyroxiphium calignis C. N. Forbes
Argyroxiphium grayanum (Hillebr.) O. Deg.
Argyroxiphium kauense (Rock & M. Neal) O. Deg. & I. Deg.
Blepharipappus scaber Hook.
Blepharizonia laxa Greene
Calycadenia fremontii A. Gray
Centromadia perennis Greene
Deinandra greeneana (Rose) B. G. Baldwin
Dubautia arborea (A. Gray) D. D. Keck
Dubautia herbstobatae G. D. Carr
Dubautia imbricata H. St. John & G. D. Carr
Dubautia laevigata A. Gray
Dubautia microcephala Skottsb.
Dubautia paleata A. Gray
Dubautia pauciflorula H. St. John & G. D. Carr
Dubautia platyphylla (A. Gray) D. D. Keck
Dubautia raillardioides Hillebr.
Dubautia sherffiana Fosberg
Harmonia stebbinsii (T. W. Nelson & J. P. Nelson) B. G. Baldwin
Hemizonia congesta DC.
Holozonia filipes (Hook. & Arn.) Greene
Lagophylla minor (D. D. Keck) D. D. Keck
Layia heterotricha (DC.) Hook. & Arn.
Madia citriodora Greene
Madia exigua (Sm.) A. Gray
Madia glomerata Hook.
Madia gracilis (Sm.) D. D. Keck & J. C. Clausen ex Applegate
Madia radiata Kellogg
Madia subspicata D. D. Keck
Osmadenia tenella Nutt.
Wilkesia hobdyi H. St. John

SPECIES BEFORE SPECIATION IS COMPLETE[1]

Peter R. Grant[2] *and B. Rosemary Grant*[2]

Abstract

The adaptive radiation of Darwin's finches in the Galapagos archipelago stands as a model of species multiplication. The radiation began two to three million years ago, and resulted in 14 species being derived from the original colonizing species. This system is highly suitable for investigating the causes of speciation because closely related species occur sympatrically in several combinations and in environments with relatively little anthropogenic disturbance. The role of natural selection and adaptation to feeding niches in the allopatric phase of speciation has been demonstrated repeatedly. In the sympatric phase of speciation, differences in song and morphology act as a premating barrier to gene exchange. This form of reproductive isolation evolves at least partly as a passive consequence or byproduct of adaptive divergence in beak morphology. Song characteristics diverge in allopatry, largely independent of beak morphology and for a variety of reasons, not all of which are well understood. The barrier to gene exchange in sympatry is not completely effective, however; species hybridize rarely, and under some circumstances the hybrids are surprisingly fit. These results challenge some current notions of species. For example, the ground finch species *Geospiza scandens* Gould and *G. fortis* Gould on the island of Daphne Major have lost morphological diagnosability, as a result of introgressive hybridization, while retaining vocal diagnosability. Speciation is a process of divergence, and therefore these two populations are currently despeciating. With a change in climatic conditions they are expected to respeciate. Such merge-and-diverge dynamics may occur frequently in hybrid zones and in relatively young radiations in habitats subject to strong environmental fluctuations.

Key words: allopatric divergence, conservation, evolutionary potential, hybrid fitness, imprinting, introgression, song, species barrier, species concept.

Two inter-related questions in evolutionary biology have been discussed intensively in the last decade. These are: what are species, and what role does hybridization play in speciation? The debate about species is about concepts and criteria (Coyne & Orr, 2004; de Queiroz, 1998, 2000; Harrison, 1998; Hey, 2001; Mayr, 2000, 2001; Orr, 2001; Shaw, 2001; Wu, 2001a, b). The debate about hybridization centers on whether it has a creative role in speciation through enhancement of multilocus genetic variation, or whether it has no effect or even retards or reverses the process (Mayr, 1942; Stebbins, 1950; Svärdson, 1970; Mecham, 1975; Raven, 1976; Arnold, 1997; Hercus & Hoffmann, 1999; Barrier et al., 2001; Barton, 2001; Martinsen et al., 2001; Ortíz-Barrientos et al., 2002; Rieseberg et al., 2003). The two subjects are inter-related because when populations hybridize, and therefore are not completely isolated reproductively from each other, the question arises as to whether they should be considered as one species or two.

We address the two issues of species and hybridization by discussing recent findings from field studies of Darwin's finches on the Galapagos islands. The studies are designed to investigate the causes of speciation within the broader context of an adaptive radiation. One key component is adaptive divergence in resource (food) exploiting traits. Three major lines of evidence demonstrate the role of natural selection in divergence (P. R. Grant & B. R. Grant, 1997a). First, populations differ ecologically on different islands that have different arrays of food resources (Abbott et al., 1977; Smith et al., 1978). Second, the particular species on an island and their beak sizes are predictable to a large extent from the food supply (Schluter & Grant, 1984). Third, when the food environment changes, evolutionary change occurs as a result of natural selection on heritable variation in beak size and shape as well as body size (Boag & Grant, 1981; B. R. Grant & P. R. Grant, 1989; P. R. Grant & B. R. Grant, 1995, 2002a).

A second key component is divergence in courtship signals and responses leading to reproductive isolation of two populations derived from one. This is the focus of our article. We address four questions: what constitutes a barrier to gene exchange between closely related species, how does it originate, how might it be breached, and what are the consequences of occasional hybridization? Answers to these questions constitute the background to a concluding discussion of species as taxonomic units.

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The Barrier to Gene Exchange

Darwin's finch species are similar in the type of nest they build and, as far as we can tell, in their courtship behavior (Lack, 1947; Ratcliffe & Grant, 1983a). Species in the same genera are similar in plumage but differ in beak morphology and song (P. R. Grant, 1999). Differences in these latter two traits would appear to be the best candidates for barriers to gene exchange and, indeed, field experiments with sympatric species in the ground finch genus *Geospiza* Gould have confirmed their potential role (Ratcliffe & Grant, 1983a, 1985).

The two sets of traits are interestingly different. Beak size and body size are polygenic traits that display high heritabilities (P. R. Grant & B. R. Grant, 2000; Keller et al., 2001), whereas songs, sung only by males, are culturally transmitted from father to son (B. R. Grant & P. R. Grant, 1996a). Bowman (1983) demonstrated with lab experiments that songs of Darwin's finches are learned, in an imprinting-like manner, between approximately day 10 and day 30 after hatching. These 20 days cover the period from the last few days in the nest to the end of the fledglings' dependence on their parents. The father sings throughout this time. Our field studies support Bowman's laboratory findings (B. R. Grant & P. R. Grant, 1989; Gibbs, 1990). They show that a strong resemblance exists between song characteristics of sons and fathers and even paternal grandfathers but not maternal grandfathers (B. R. Grant & P. R. Grant, 1996a).

Often exceptions are more revealing than the rule. Imprinted traits, being learned, are subject to misimprinting if young birds are exposed to the song of a different species rather than, or more than, the father's song, during the short sensitive period of learning. This has been observed in a study of *Geospiza fortis* Gould (medium ground finch) and *G. scandens* Gould (cactus finch) on the small island of Daphne Major (B. R. Grant & P. R. Grant, 1996a, 1998; P. R. Grant & B. R. Grant, 1997b). Misimprinting happens rarely, in three types of circumstances. It occurs when (1) a father dies and the offspring learn the song of the nearest natal neighbor, which can be the bird of another species; (2) nests of two species are close together and one male sings louder, more persistently, and chases off the other male; and (3) a nest with one of the original eggs in it is taken over by a pair belonging to another species, the egg hatches, and the nestling is fed by and learns the song of its foster father.

Introgressive Hybridization

Following the fates of 16 misimprinted finches has revealed that they mate mainly according to song type and not morphology, and consequently hybridize and produce hybrid offspring. If they are males, they sing the same single song as sung by their fathers and mate with a female whose father sang that song type (P. R. Grant & B. R. Grant, 1997c). If they are females, they choose a mate that sings the same song as their fathers'. Even though F_1 hybrids and backcrosses are morphologically intermediate between the parental species, they breed strictly according to song type (B. R. Grant & P. R. Grant, 1998). Thus, through occasional misimprinting, introgression of genes occurs in both directions between *Geospiza fortis* and *G. scandens*.

Hybrid Fitness

Hybrids have been formed rarely (~1% of breeding pairs are interspecific), but approximately continuously, throughout our 30-year study on Daphne Major. However, in the first 10 years none survived to breed. At this time we considered two possible reasons for their failure: genetic incompatibility and ecological insufficiency. Few birds, hybrids and non-hybrids, survived the generally poor feeding conditions in the early years. Hybrids, with their intermediate beak sizes, were unable to crack the large and hard seeds of *Tribulus cistoides* (L.) that the more robust-billed *Geospiza fortis* were feeding on, and they took significantly longer to crack open the seeds of *Opuntia echios* Howell, which is the main dry-season food of *G. scandens* (B. R. Grant & P. R. Grant, 1996b). After the unprecedentedly high rainfall in the El Niño year of 1983, the ecological conditions on the island changed dramatically (P. R. Grant et al., 2000b). The previously common large and hard seeds of *T. cistoides* and *O. echios* diminished in the seed bank, these plants having been smothered by vines and other small-seed producing plants. Under these altered conditions of an abundance of small and soft seeds, hybrids and backcrosses survived to reproduce. Therefore, their previous failure is attributable to ecological insufficiency and not to genetic incompatibility.

After 1983, hybrids survived as well as, if not better than, their parental species, and reproduced as well as them, there being no difference in number of eggs, nestlings, or fledglings produced (P. R. Grant & B. R. Grant, 1992). We detected no loss of fitness in the F_1 and backcross generations in terms of relatively poor survival, mating success, or reproduction (P. R. Grant & B. R. Grant, 1992; B. R. Grant & P. R. Grant, 1998; P. R. Grant et al., 2003; but see Barton, 2001).

Implications of Introgression

There are two important implications of the documented introgressive hybridization. First, post-

mating isolation appears not to have evolved between these and other pairs of ground finch species (B. R. Grant & P. R. Grant, 1989, 1998; P. R. Grant et al., 2005). Even more distantly related species of Darwin's finches have been known, or suspected, to hybridize without a recorded loss of fitness (P. R. Grant, 1999). This is not surprising. According to comparative evidence from other bird species it takes more than two million years for post-zygotic incompatibilities to evolve (Price & Bouvier, 2002). All, or almost all, of the adaptive radiation of Darwin's finches took place in less than this time (P. R. Grant, 1999; Sato et al., 2001; Burns et al., 2002). Second, hybridization and backcrossing has enhanced the evolutionary potential of these two species by increasing additive genetic variances while reducing constraints from genetic correlations (P. R. Grant & B. R. Grant, 1994). The reduction in strength of genetic correlations between beak size traits is due to the interspecific differences in allometries. In principle, a third implication is that hybrids have the potential to invade new habitats (Lewontin & Birch, 1966) and even form a new species in another environment (see Rieseberg, 2006 this issue). We conjecture that introgressive hybridization may have contributed to speciation in the past, although we lack evidence that this happened in any particular case.

The Origin of a Barrier to Gene Exchange

Based on these findings, reproductive isolation of Darwin's finches is explained by a theory of discrimination by song in association with morphology that is learned in a sexual imprinting-like process early in life (B. R. Grant & P. R. Grant, 2002; P. R. Grant & B. R. Grant, 2002b).

We now apply contemporary findings from Daphne to the question of how reproductive isolation evolves, using as a framework the allopatric model of speciation. The model invokes ecological adaptation in allopatry as a requirement for the establishment of sympatric coexistence of two species derived from one. For this there is plenty of evidence (see introduction to this article). A total or near-total lack of interbreeding is another requirement. The model invokes an allopatric origin of a pre-mating barrier to gene exchange. Experiments show that some degree of differentiation in the cues used in mate choice must arise allopatrically.

Experiments with museum specimens from different islands were conducted to simulate the secondary contact phase of the speciation cycle (Ratcliffe & Grant, 1983b). In a variety of tests with different ground finch species, we consistently found weak or no discrimination between an immigrant and a (resident) member of the responding bird's own population when beak differences between them were small, and strong discrimination when the differences were large. Acoustic cues were controlled for in these experiments by eliminating them; dead museum specimens do not sing!

Playback experiments without museum specimens as visual cues showed that ground finches discriminate acoustically between residents and immigrants in a similar way to their visual discrimination: they discriminate when differences are large and fail to do so when they are small (Ratcliffe & Grant, 1985).

The morphological barrier arises as a result of adaptation. As such it conforms to an old idea dating back at least 65 years to Dobzhansky (1937) that reproductive isolation originates as a byproduct of adaptive differentiation. We know less about how the song barrier arises (B. R. Grant & P. R. Grant, 2002; P. R. Grant & B. R. Grant, 2002b). One possibility is that song characteristics covary with beak size for biomechanical reasons, affecting trill rate and the range of frequencies of individual notes (Podos, 1997) and, therefore, when beak size changes adaptively, songs change as a passive consequence. There is some supporting evidence (Podos, 2001); nevertheless, correlated effects of beak change appear to be insufficient to set up a barrier to gene exchange because coexisting sister species of *Geospiza* do not differ discretely in these two song features (B. R. Grant & P. R. Grant, 2002). In contrast to this interspecific similarity, populations of the same species may differ substantially in songs independent of beak size differences (P. R. Grant et al., 2000a). The hypothesis is undermined by the ability of sympatric species with different beak sizes to sing each other's songs with scarcely altered characteristics (Bowman, 1983; B. R. Grant & P. R. Grant, 1989, 1998; P. R. Grant & B. R. Grant, 1997b, c). Correlated effects of body size changes may also contribute to a barrier through an influence on frequency characteristics of songs (Bowman, 1983). Since beak size and body size generally covary, a third, and more realistic, hypothesis is that they are jointly involved in determining characteristics of songs and hence the barrier to interbreeding. Another possibility is that a new song type may originate as a cultural mutation through miscopying of father's song and increases in frequency by chance or selectively. A selective advantage may arise if the songs transmit better in the new environment and, as a result, more effectively repel intruding males or attract females. The origin of reproductive isolation is still not fully understood, and these possibilities need further investigation.

Adaptive Diversification through Repeated Speciation

The foregoing explanation of how two species are formed from one serves as a basis for explaining the adaptive radiation as a whole (P. R. Grant & B. R. Grant, 2002c). Fourteen species evolved from a single ancestral species by a simple repetition of the process of division, with the species produced at each step differing according to the particular ecological circumstances that guided each pathway. This was our starting point (P. R. Grant, 1981, 1999). Furthermore, we believed most niche space would be occupied in the early history of the radiation, with later speciation resulting in gap-filling, as illustrated recently by Jonathan Losos and colleagues with Caribbean *Anolis* Daudin lizards (Harmon et al., 2003; Losos et al., 2006 this issue). For experimental and observational work we concentrated on the ground finch twigs of the phylogenetic tree, because these species are most similar to each other and have been genealogically separated for a short time. To see if the same processes of divergence in morphology and song occurred early in the history of the radiation, we have gone to the base of the tree. There, five years ago, we encountered a surprising fact. The initial divergence is frozen at the allopatric stage. Reconstructions that have used both mitochondrial and nuclear genetic markers (Freeland & Boag, 1999a, b), including microsatellite DNA (Petren et al., 1999), show a basal split between two groups of warbler finches that are now allopatric on different sets of islands (Petren et al., 1999; Tonnis et al., 2005).

Why have they remained allopatric? What has prevented them from establishing sympatry? We do not have complete answers to these questions. Part of any answer requires greater knowledge than we have of ecological opportunity for joint occupancy of an island. Another part requires knowledge of potential reproductive isolation, and this we do have.

Morphologically the two groups of warbler finches are similar; correspondingly, they are similar ecologically as well. They also share the peculiar feature of reversed sexual dimorphism in beak length, in which trait they differ from all other Darwin's finch species and from all continental relatives (P. R. Grant & B. R. Grant, 2003). They differ from each other to some extent in plumage color and beak size, but scarcely enough to prevent them from interbreeding to judge from differences in pairs of sympatric species of Darwin's finches. However, their songs do differ (B. R. Grant & P. R. Grant, 2002). With a focus on the question of the origin of reproductive isolation, we performed a set of playback experiments similar to earlier ones in which we simulated immigration of birds from another island (B. R. Grant & P. R. Grant, 2002; P. R. Grant & B. R. Grant, 2002c). On the island of Genovesa, occupied by *Certhidea fusca* Sclater, we tested birds with their own songs, songs from another population of *C. fusca*, and songs from two populations of *C. olivacea* Gould. We performed similar experiments with the same playback tapes on an island, Santa Cruz, occupied by *C. olivacea*. We expected to find strong discrimination, manifested in the pattern of contrasts shown in Figure 1 (above). Instead we found little evidence of discrimination of heterotypic (heterospecific) song on either island (Fig. 1, below). This is fascinating because it contrasts with clear discrimination between sympatric and younger species. One would have thought warbler finches of the two groups have surely had enough time to diverge in both beak morphology and song to enable them to coexist without interbreeding. Yet the implication of the playback results is that the oldest (allopatric) lineages would interbreed, whereas the youngest (sympatric) ones do not, or do so very rarely. Moreover, the genetic evidence tells us that despite their apparent potential to exchange genes, they have not done so, at least not to an appreciable extent, for a long time (Petren et al., 2005).

There are three other implications of this striking contrast (B. R. Grant & P. R. Grant, 2002). The first is that rates of song and morphological divergence vary among the species; hence, the rate of evolution of sexual isolation varies considerably and is not a simple function of time. The second is that either divergence in song is accelerated in sympatry, perhaps by selective reinforcement of initial differences if offspring of mixed matings are at a selective disadvantage, or establishment of sympatry is made possible only by the acquisition of pronounced song differences in allopatry. The third implication is that a knowledge of neutral genetic differences among taxa in young radiations like Darwin's finches is not enough for inferring their potential to interbreed and exchange genes. Geographical, ecological, and behavioral information is needed as well (Petren et al., 2005; Tonnis et al., 2005). Ferguson (2002) has argued similar points more generally.

Species Reconsidered

According to Cracraft (2002), the first great question of systematic biology is, what is a species? Templeton (1989) has suggested this question must be answered before the process of species formation can be investigated. Like other evolutionary biologists attempting to understand speciation, we have not heeded this advice. Instead of defining the species we study, we have found it sufficient to simply invoke the biological species concept with its emphasis on the

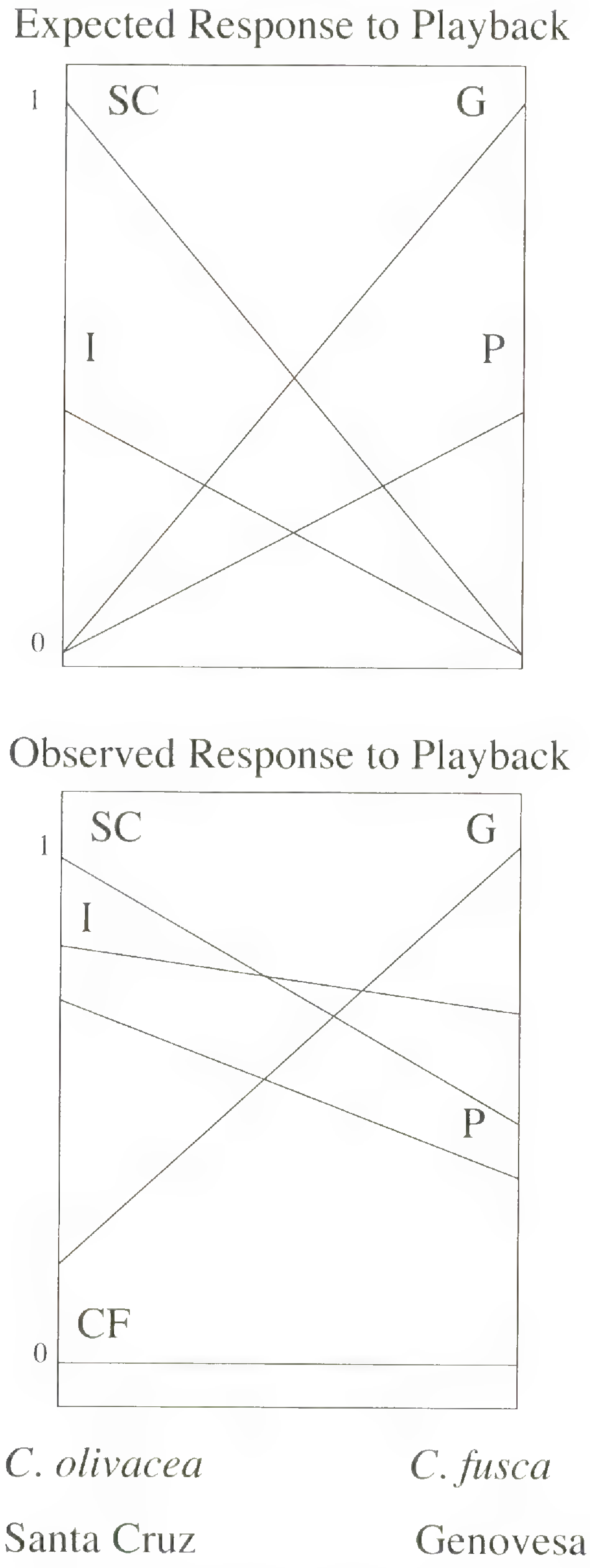

Figure 1. Expected (above) and observed (below) responses of warbler finches on Santa Cruz (*Certhidea olivacea*) and Genovesa (*C. fusca*) to playback of songs recorded on Santa Cruz (SC), Isabela (I), Genovesa (G), and Pinta (P). Responses are scaled to 1.0 on each island where experiments were conducted. Controls were Cassin's finch (CF) songs recorded in North America. Populations on Santa Cruz and Isabela belong to the *C. olivacea* lineage, and populations on Genovesa and Pinta belong to the *C. fusca* lineage. Figure based on B. R. Grant & P. R. Grant, 2002: fig. 3 (© 2002 by the University of Chicago).

evolution of reproductive isolation and not on classification (Harrison, 1998; Hudson & Coyne, 2002). De Queiroz (1998: 63) has followed the paleontologist G. G. Simpson (1961) in arguing "there is really only one general species concept in modern systematic and evolutionary biology—species are segments of population level evolutionary lineages." He then offers an important distinction: "A *species concept* is an idea about the kind of entity represented by the species category, that is, about the kind of entity designated by the term *species*. A *species criterion* is a standard for judging whether a particular entity qualifies as a member of the species category, that is, for judging whether a particular entity is or is not a species" (de Queiroz, 1998: 65). This neatly bypasses the plethora of tangled arguments about species concepts and allows debate to be focused on how species should be recognized.

Ernst Mayr (1942) defined species as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such populations. The criterion here is clearly one of interbreeding. Application of this definition to individuals in order to refer them to species has repeatedly encountered practical difficulties with allopatric populations and with populations connected occasionally or rarely by interbreeding (Zink & McKitrick, 1995; see Avise & Wollenberg, 1997, and Wake, 2006 this issue). These practical difficulties have been faced head-on by ornithological systematists. For example, the Taxonomic Subcommittee of the British Ornithologists' Union confronted them in drawing up guidelines to assist in the assessment of species rank for the British Bird Species List. They started with a position statement: "If we define species as population lineages maintaining their integrity with respect to other such lineages through time and space, this means that species are diagnosably different (otherwise we could not recognize them), reproductively isolated (otherwise they would not maintain their integrity upon contact) and members of each (sexual) species share a common mate recognition and fertilization system (otherwise they would be unable to reproduce)" (Helbig et al., 2002: 519). Then they followed with two recommendations. First, "Diagnosable taxa will be ranked as species if they are broadly sympatric, i.e., over areas beyond the average natal dispersal distance of the species involved,. . . and do not hybridize. . . , or hybridize only rarely, so that gene flow between them either does not occur (because hybrids are sterile or do not backcross for other reasons) or occurs at such a low frequency (often difficult to detect) that it is unlikely their gene pools will ever merge. . . " (Helbig et al., 2002: 522). Second, allopatric populations

should be considered different species "if they have diverged to the extent that merging of their gene pools in the future is unlikely" (Helbig et al., 2002: 519), whereas, "predictions about possible reproductive isolation between allopatric taxa that differ only slightly (e.g., in size or darkness of plumage) are very uncertain. Such taxa are best treated as subspecies" (Helbig et al., 2002: 519). On the basis of the latter, and recognizing our ignorance of post-mating compatibility, the warbler finches are best treated as subspecies. We consider them to be well-differentiated genetic lineages.

These prescriptions for sympatric and allopatric species fit very well with our past 30 years of thinking and practice based on the biological species concept and notwithstanding the fuzziness (Harrison, 1998; Hey, 2001; Lee, 2003) of species boundaries caused by rare hybridization. The prescriptions clearly apply to sexually reproducing species generally and not just to birds. Nevertheless Darwin's finch studies expose two hidden problems with the diagnosis of sympatric species. First, species may lose diagnosability. Second, if they do it is an arbitrary matter to decide when they lose their species status.

At the beginning of our study on Daphne Major *Geospiza fortis* and *G. scandens* were diagnosably different on morphological criteria (P. R. Grant, 1993). With hybridization, backcrossing, and natural selection occurring, the populations have converged in morphology and are now more similar than they were at the beginning (P. R. Grant & B. R. Grant, 2002a; P. R. Grant et al., 2004). They are no longer 100% diagnosably different on the same morphological criteria. Have they lost their species status in a couple of decades? They are merging, but very slowly. Members of the two populations can still be recognized by us on the basis of the song they sing (males) or the song of their mates (females), as well as by beak morphology in almost all instances. The problem that this poses for the delineation of species is that song is a learned, culturally inherited, trait, without a genetic basis in many species of birds, and yet "...characters used in diagnosis must be the result of evolution: they must be genetically based and not merely caused by environmental factors such as nutrition" (Helbig et al., 2002: 520). A way out of this dilemma is to broaden the basis of diagnosis by recognizing that cultural inheritance may be as important as genetic inheritance in trans-generational maintenance of biologically important traits used in reproduction. We recommend this because song is the cultural equivalent of the Y chromosome in these birds; paternally inherited, non-recombining, and subject to change only by mutation, cultural mutation in this case. Song variation has been found to be useful in systematic studies of other groups of birds (Ahlström & Ranft, 2003).

The second problem has no simple solution. "We do not know of a single documented case of breakdown of reproductive isolation (i.e., a reversal to full reproductive compatibility between species that were incompatible before) in any class of organism" (Helbig et al., 2002: 521). However, Kat (1985) described a possible case of breakdown of reproductive isolation with two species of *Anodonta* L. freshwater mussels. According to fossil evidence, they coexisted without interbreeding about 200,000 years ago, and now at the same locality they hybridize relatively commonly. The two finch species on Daphne may become the first exception to be witnessed in progress. At present they are on a reversed course of speciation (P. R. Grant et al., 2004), in fact they are *despeciating*, and the point at which they should no longer be considered two species, but only one, is arbitrary. Morphological and genetic convergence could easily be reversed if there is a change in climate and food composition, in which case they will be *respeciating*. Many other pairs of taxa, not just Darwin's finches, might go through similar merge-and-diverge oscillations, as in some shifting hybrid zones (e.g., Carney et al., 2000), possibly also in young adaptive radiations such as the silversword alliance in Hawaii (Barrier et al., 2001; Baldwin, this volume) and cichlid fish in the African Great Lakes (Salzburger et al., 2002; Smith & Kornfield, 2002).

Such fluidity can be bewildering to those who recognize species by inferred ancestry rather than by interbreeding and its consequences. For instance Zink (2002), basically restricting attention to the lack of differentiation in mitochondrial DNA among species (Freeland & Boag, 1999a, b; Sato et al., 1999) that are upheld by other criteria, has argued there are far fewer species of Darwin's finches than are currently recognized, perhaps only half. Aside from an unfortunate reliance on a single, potentially misleading, molecule (Ballard et al., 2002; Hudson & Coyne, 2002; Ferguson, 2002; Machado & Hey, 2003; Rokas et al., 2003), a view such as this overlooks the fact that as many as 10 species coexist on the same island, ecologically differentiated, morphologically recognizable, and reproductively isolated by song and morphology (P. R. Grant, 1999).

These problems illustrate the well known fact that systematics deals with discrete categories, whereas evolutionary change is a continuous and gradual process (Harrison, 1998; Hey, 2001; Hey et al., 2003). Darwin's finches are valuable to evolutionary biologists precisely because they so well exemplify the graded nature of evolutionary transitions. They are challenging to systematists for the same reason.

Conservation of Biodiversity

Darwin's finches are valuable to conservation biologists for another reason. They deliver a message about preserving biodiversity: since species, like their environments, are continually changing, both must be conserved to allow adaptation to further change. For any given focal species, or evolutionarily significant population of the species (Hey et al., 2003), other species in the community are part of the environment, be they food, competitors, predators, or parasites. This is especially clear in the case of interbreeding species, because their ecological and evolutionary future depends to some extent upon the genes they exchange with each other (Cade, 1983; B. R. Grant & P. R. Grant, 1989; Rhymer & Simberloff, 1996). It is clear with competitor species that persist only when predators prevent one species from competing the others to extinction (Paine, 2002). It is clear from the dependence of finches (B. R. Grant & P. R. Grant, 1989) and primates (Terborgh, 1983) on one or two specific food sources at seasons of acute food limitation. And it is clear from the myriad indirect effects that are manifested in the trophic networks of complex communities (e.g., Wootton, 1993; Dayton, 2003). Thus ecosystems, rather than individual species, are the appropriate units in programs of long-term conservation of biodiversity.

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POLYPHYLY IN *GUETTARDA* L. (RUBIACEAE, GUETTARDEAE) BASED ON nrDNA ITS SEQUENCE DATA[1,2]

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Abstract

The genus *Guettarda* (Guettardeae–Rubiaceae) comprises approximately 150 species, ranging from eastern Africa through the islands of the Indian and Pacific Oceans to the Neotropics. Sequence data from the nuclear ribosomal DNA internal transcribed spacer (ITS) region were used to test the monophyly of *Guettarda* and its relationships to closely related genera within Guettardeae. The results indicate that *Guettarda* and two smaller genera, *Antirhea* and *Stenostomum*, are polyphyletic. Most *Guettarda* species fall into two distinct groups: a Neotropical lineage that also includes the widespread Indo-Pacific strand species *G. speciosa* (the type of the genus), and a New Caledonian lineage that, along with *Antirhea* and *Timonius*, comprises a dioecious Paleotropical clade. The Hawaiian endemic *Bobea*, traditionally considered close to *Timonius* and assumed to be of Old World origin, appears to be more closely related to Neotropical *Guettarda* species, suggesting that dioecy may have evolved twice within the tribe. The use of traditional gynoecium characters to delimit genera within Guettardeae is not congruent with the ITS phylogeny; other features, such as inflorescence architecture, sexual system, and palynology, appear to correlate more closely with the molecular phylogeny.

Key words: biogeography, dioecy, *Guettarda*, Guettardeae, islands, ITS, Neotropics, Paleotropics, Rubiaceae, systematics.

Rubiaceae, one of the largest families of flowering plants with ca. 13,000 species and 650 genera (Delprete, 2004), comprise 44 tribes (Robbrecht, 1988) currently assigned to three subfamilies (Bremer & Jansen, 1991; Bremer et al., 1995; Bremer, 1997; Bremer et al., 1999). The genus *Guettarda* L. and its relatives have been regarded for most of the last two centuries as a fairly clear-cut group, generally recognized as tribe Guettardeae, and sometimes even as a distinct subfamily under the invalid name Guettardoideae [= Antirheoideae] (Verdcourt, 1958; Bremekamp, 1966). While assigned to subfamily Antirheoideae by Robbrecht (1988), a series of recent molecular phylogenetic studies have shown that Guettardeae are best placed in Cinchonoideae (Bremer & Struwe, 1992; Bremer et al., 1995; Bremer, 1996; Rova, 1999; Rova et al., 2002; Andersson & Antonelli, 2005).

As part of a systematic study of the New Caledonian species of *Guettarda*, a molecular phylogenetic analysis was conducted to evaluate the monophyly of this widespread tropical genus, whose definition has varied considerably. Originally described by Linnaeus (1753) as monotypic, *Guettarda* has progressively grown with the description of additional species and the inclusion of at least five other genera: *Matthiola* L. and *Laugieria* Jacq. (Lamarck, 1792); *Antirhea* ("*Antirrhoea*," Mueller, 1875); and, more recently, *Tournefortiopsis* Rusby and *Dicrobotryum* Willd. ex Roem. & Schult. (Standley, 1931). The broadest definition of *Guettarda* by far was that of Baillon (1879, 1880), who included all Guettardeae species

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known at the time. Schumann (1891) rejected Baillon's ideas and restricted the circumscription of *Guettarda*, excluding taxa usually placed in *Antirhea* and *Laugieria*. While Schumann's concept has been followed by most authors since (e.g., Standley, 1934; Bremekamp, 1966; Airy Shaw, 1973; Steyermark, 1972, 1974; Robbrecht, 1988), a modern comprehensive review of the genus is lacking.

Guettarda is currently regarded as a large, nearly pan-tropical genus of trees and shrubs. It is characterized by flowers with usually imbricate corolla lobes, 2- to 9(to 20)-locular fruits with a stony endocarp and one seed per locule, and a non-persistent calyx. In the Neotropics, *Guettarda* is thought to comprise anywhere from nearly 80 (Taylor et al., 2004) to more than 130 species (Andersson, 1992), and is morphologically quite heterogeneous, including taxa originally described or placed in several genera once regarded as distinct, e.g., *Dicrobotryum*, *Laugieria*, *Matthiola*, and *Tournefortiopsis*. Furthermore, the inclusion of *Antirhea* (or *Stenostomum*, to which Neotropical *Antirhea* species are currently assigned) can also be inferred based on the recent placement of the South American species *A. surinamensis* (described by Bremekamp, 1959) in synonymy under *Guettarda acreana* K. Krause by Taylor et al. (2001).

In the Paleotropics, a single, common, coastal species (*Guettarda speciosa* L.), which ranges from eastern Africa to Polynesia, accounts for most of *Guettarda*'s broad distribution. The other Old World species (ca. 25 in all) are almost exclusively narrow endemics on New Caledonia and comprise a morphologically diverse group. These were assigned to *Guettarda* by Baillon (1879) and Guillaumin (1948) in accordance with their broad concept of the genus, although they differ from its other members by several important characters including a dioecious sexual system and a persistent calyx. As currently circumscribed, the genus *Guettarda* thus has two main centers of diversity, the Neotropics and New Caledonia, showing an unusual trans-Pacific distribution shared with only a few other genera of Rubiaceae, such as *Augusta* Pohl sensu Kirkbride (1997) (including *Lindenia* Benth.) (Robbrecht, 1988).

Recent molecular phylogenetic studies have provided little evidence regarding the monophyly of *Guettarda*. Molecular sequence data for the genus are scarce, and, apart from the inclusion of a few species in family-level phylogenies, the only taxa studied to date are those used by Rova (1999) and Rova et al. (2002), who examined *rps*16 and *trn*L-F sequences of a limited number of exemplar taxa. However, due to insufficient levels of sequence variation, trees based on these markers place the six *Guettarda* species they sampled in a polytomy along with several allied genera, viz. *Chomelia*, *Malanea*, *Neolaugeria*, *Stenostomum* (referred to as *Antirhea*), and *Timonius*. Considering the wide range of interpretations (often contradictory) of relationships based on the morphological, biogeographical, and molecular data, it seems opportune to examine more closely the phylogenetic status of *Guettarda*, as currently defined, and its affinities with its apparent close allies.

Guettarda and the other genera currently included in Guettardeae (Table 1) are generally grouped together based on a set of common characters including: a woody habit, entire interpetiolar stipules (divided in *Neoblakea*), axillary inflorescences (terminal in *Dichilanthe*, *Machaonia*, and *Neoblakea*), a single, apically attached, pendulous ovule in each cell of the ovary, fleshy fruits with 2 to many unilocular pyrenes or a plurilocular endocarp or putamen (dry capsular fruits in *Machaonia*), and elongated seeds with poorly-developed endosperm (Robbrecht, 1988). Using this definition, the tribe contains perhaps 12 to 15 genera and more than 500 species, ranging in distribution from coastal East Africa to Polynesia and the Neotropics (Achille, unpublished data). The analysis of Rova et al. (2002) using sequence data from the chloroplast *trn*L intron and *trn*L-F spacer suggested a much broader circumscription of Guettardeae (Table 1) that includes several genera formerly placed in two other tribes, Isertiae and Rondeletiae. However, the expanded notion of Guettardeae proposed by Rova et al. (2002) seems problematic because the additional taxa they included have morphologies strikingly different from those of Guettardeae s. str., as reflected by the fact that these elements (whose distinctive features include strictly terminal inflorescences, mostly pluriovulate locules and capsular fruits, or sometimes sub-capsular fruits in *Gonzalagunia*) were placed by Robbrecht (1988) in subfamily Cinchonoideae, whereas Guettardeae were assigned to Antirheoideae.

Within Guettardeae (sensu Robbrecht), several elements appear to be most closely related to *Guettarda* (as currently circumscribed), together comprising core Guettardeae (as defined in Table 1): viz. *Antirhea* (including *Guettardella*), *Bobea*, *Chomelia*, *Guettarda*, *Malanea*, *Neolaugeria*, *Ottoschmidtia*, *Pittoniotis*, *Stenostomum*, and *Timonius*. These 10 genera form a morphologically homogeneous group whose recognition is consistent with available molecular data. In the phylogenies from Rova (1999) and Rova et al. (2002), the core Guettardeae they sampled (except *Bobea*) comprise a strongly supported monophyletic group, while the remainder of the tribe (sensu

Table 1. Genera included in Guettardeae by Robbrecht (1988) and in the "Guettardeae" s.l. clade in the phylogenies of Rova (1999) and/or Rova et al. (2002); those retained in core Guettardeae (as defined here) are indicated in the right column. excl. = excluded; n.s. = genus not studied.

Genus	Guettardeae sensu Robbrecht (1988)	Guettardeae clade of Rova (1999) & Rova et al. (2002)	Genera in core Guettardeae (as defined here)
Allenanthus Standl.	excl.	*Allenanthus*	
Antirhea Comm. ex Juss.[1]	*Antirhea*	n.s.	*Antirhea*
Arachnothryx Planch.	excl.	*Arachnothryx*	
Bobea Gaudich.	*Bobea*	excl.	*Bobea*
Chomelia Jacq.	*Chomelia*	*Chomelia*[2]	*Chomelia*
Cuatrecasasiodendron Standl. & Steyerm.	excl.	*Cuatrecasasiodendron*	
Dichilanthe Thwaites	*Dichilanthe*	n.s.	
Gonzalagunia Ruiz & Pav.	excl.	*Gonzalagunia*	
Guettarda L.	*Guettarda*	*Guettarda*[2]	*Guettarda*
Guettardella Champ. ex Benth.	*Guettardella*	n.s.	within *Antirhea*
Javorkaea Borhidi & Komlodi	excl.	*Javorkaea*	
Machaonia Bonpl.	*Machaonia*	*Machaonia*	
Malanea Aubl.	*Malanea*	*Malanea*[2]	*Malanea*
Neoblakea Standl.	*Neoblakea*	*Neoblakea*	
Neolaugeria Nicolson	*Neolaugeria*	n.s.	*Neolaugeria*
Ottoschmidtia Urb.	*Ottoschmidtia*	n.s.	*Ottoschmidtia*(n.s.)
Rogiera Planch.	excl.	*Rogiera*	
Pittoniotis Griseb.	*Pittoniotis*	n.s.	*Pittoniotis*
Stenostomum C. F. Gaertn.	within *Antirhea*	*Antirhea*[2,3]	*Stenostomum*
Timonius DC.	*Timonius*	*Timonius*[2]	*Timonius*

[1] Sensu Chaw & Darwin (1992).
[2] Genera assigned to the core Guettardeae clade by Rova (1999) and/or Rova et al. (2002).
[3] The authors actually sampled only one species, *Antirhea acutata* (DC.) Urb., which is currently placed in *Stenostomum* (Borhidi & Fernandez, 1993–1994).

Robbrecht, 1988), except *Dichilanthe* (which was not sampled), are scattered among a paraphyletic group. Furthermore, core Guettardeae, as circumscribed here, which correspond to Baillon's (1879, 1880) broadly defined *Guettarda*, display none of the distinctive features (mentioned above) that characterize *Dichilanthe*, *Neoblakea*, *Machaonia*, or the genera newly included in the tribe by Rova (1999) and Rova et al. (2002).

Although *Bobea* has always been included in Guettardeae, Rova (1999) suggests that it would have to be excluded in order to render the circumscription of the tribe (s.l.) monophyletic. Morphology, however, provides very strong support for the inclusion of *Bobea* within the core group of Guettardeae. *Bobea* is hardly distinguishable from *Timonius*, where it was placed in synonymy by Candolle (1830), and Baillon (1880) included both genera within *Guettarda* s.l. More recently, Darwin and Chaw (1990) regarded *Bobea* as distinct, but closely related to *Timonius* on the basis of morphology. In the field, individuals of *Bobea* are immediately recognizable as belonging to Guettardeae on the basis of fruit structure and overall morphology (pers. obs.). Notwithstanding Rova's (1999) suggestion, we have thus provisionally chosen to regard *Bobea* as a member of core Guettardeae.

Circumscriptions of the genera comprising core Guettardeae have varied widely from one treatment to another. Two genera, *Antirhea* and *Timonius*, in addition to *Guettarda* itself, play a central role in the group, as most species have at one time or another been associated with at least one of them. The Neotropical genus *Chomelia* (including *Anisomeris* C. Presl) comprises ca. 50 species and may be associated with *Guettarda* (Taylor et al., 2004), as the two are difficult to distinguish from one another on the basis of unequivocal characters. For example, Schumann (1891), Standley (1934), and Steyermark (1974) separated *Chomelia* from *Guettarda* on the basis of corolla aestivation (valvate vs. imbricate, respectively), but Burger and Taylor (1993) recognized both aestivation types in *Chomelia*. Furthermore, *trn*L-F sequence data, although limited, suggest that the two genera are related (Rova et al., 2002), as the only *Chomelia* sampled (*C. tenuifolia* Benth.) clusters with one of the five *Guettarda* species (*G. crispiflora* Vahl).

Antirhea (including *Guettardella*), *Neolaugeria*, *Stenostomum*, and *Pittoniotis* appear to comprise

a complex distributed in the Neotropics and the Indo-Pacific region, characterized by mostly 4 to 5 imbricate corolla lobes, 2 to 12 united pyrenes, and a persistent calyx. All the Paleotropical species in this group appear to be dioecious, a fact that was not discovered until recently (Chaw & Darwin, 1992). The monotypic, Neotropical genus *Pittoniotis*, described by Grisebach (1858), is readily distinguished by its long-exserted stamens, perfect flowers, and paniculate inflorescences. However, Hemsley (1881) transferred *Pittoniotis* to *Antirhea*, a decision that has been followed by some authors (Schumann, 1891; Dwyer, 1980). Hooker (1873) merged *Stenostomum*, a Caribbean genus, and *Guettardella*, a small South Asian genus, into *Antirhea*. Most subsequent authors have regarded *Stenostomum* and *Antirhea* as congeneric (e.g., Schumann, 1891; Standley, 1934; Bremekamp, 1966; Airy Shaw, 1973; Steyermark, 1974; Robbrecht, 1988). According to this broad generic circumscription, *Antirhea*, like *Guettarda*, exhibits an unusual trans-Pacific distribution.

Recently, Jansen (1984) restricted *Antirhea* to two species from the Mascarene Islands and Madagascar, and assigned all the other Old World species to *Guettardella*. His generic delimitations were based largely on the number of flowers per inflorescence, number of ovary cells, geographic distribution, and also an erroneous interpretation of floral sexuality. By contrast, Chaw and Darwin (1992) retained all the Old World species in *Antirhea* (36 species), within which they distinguished three subgenera, *A.* subg. *Antirhea*, *A.* subg. *Guettardella* (Champ. ex Benth.) Chaw, and *A.* subg. *Mesocarpa* Chaw, while tentatively suggesting that *Stenostomum* represents a distinct genus characterized by hermaphroditic, (4 to)5-merous flowers, ebracteolate inflorescences, and a Neotropical distribution. Following their suggestion, Borhidi and Fernandez (1993–1994) formally transferred the 39 American species of *Antirhea* to *Stenostomum*, and reduced *Neolaugeria* (4 to 6 Caribbean species, distinguished by the united stipules and the 4- to 6-locular ovary) to a section of *Stenostomum*. However, Moynihan and Watson (2001) rejected the inclusion of *Neolaugeria* in *Stenostomum* based on phylogenetic evidence from ITS sequence variation of three species of *Neolaugeria* and one of *Stenostomum*.

The large genus *Timonius* is traditionally characterized by having fruits with separate pyrenes, although this feature is also encountered in *Bobea*. *Timonius* comprises more than 180 species (Darwin, 1994) distributed from the Seychelles to Polynesia and from the Philippines to northern Australia. It is morphologically heterogeneous, but is classically interpreted to include all dioecious Guettardeae with valvate corolla lobes and separate pyrenes. *Bobea* comprises four species endemic to Hawaii (Darwin & Chaw, 1990), which differ mostly from *Timonius* by the presence of imbricate corolla lobes.

Finally, two Neotropical genera, *Ottoschmidtia* and *Malanea*, stand out because their circumscriptions have rarely been questioned. *Ottoschmidtia* (3 species) is easily separated from other Guettardeae by its 2-locular ovary and zygomorphic corollas. *Malanea*, with ca. 35 species (Taylor et al., 2004), is recognized by its twining habit, paniculate to spiciform inflorescence, exserted stamens, and stipules with a distinctive morphology, although Taylor et al. (2004) regard the distinction between *Malanea* and *Chomelia* as unclear.

In an effort to evaluate the phylogenetic status of *Guettarda*, as currently defined, we have endeavored to include a representative group of species belonging to the genera of core Guettardeae. Our study employs DNA sequences from the internal transcribed spacer region (ITS, spacer 1 & 2, and *5.8S* gene between the nuclear ribosomal DNA *18S–26S* genes). Using a broad sampling of 21 species of *Guettarda* (as currently circumscribed) and 21 species belonging to 10 other genera of Guettardeae (sensu Rova, 1999), we thus (1) evaluate the monophyly of *Guettarda*; (2) provide some insights regarding the phylogenetic status of other core genera in relation to *Guettarda*, especially those whose circumscriptions have varied widely; and (3) attempt to identify morphological characters that might prove valuable for further taxonomic and phylogenetic studies within Guettardeae. We have also examined the geographic distributions of *Guettarda* and *Antirhea* in light of the results of our phylogenetic analysis, as these two genera are among the only Rubiaceae to exhibit a disjunct, nearly pantropical distribution.

Materials and Methods

Taxon Sampling

To ensure the best possible representation of infrageneric groups within *Guettarda*, for which no comprehensive infrageneric treatment is available, we delimited informal morphological groups on the basis of examination of herbarium material at P and NY, field observations made by the first author in New Caledonia, and information gathered from the literature (in particular Howard, 1989; Standley, 1934; Standley & Williams, 1975). Furthermore, we attempted to include species from various phytogeographical subdivisions of the Neotropical regions, as defined by Andersson (1992). We have also sought to sample, as exhaustively as possible, at the generic

(and sometimes infrageneric) level within the other core genera of Guettardeae. To delimit infrageneric groups, we consulted the treatments of *Antirhea* by Chaw and Darwin (1992) and *Stenostomum* by Borhidi and Fernandez (1993–1994), and the partial revisions of *Timonius* by Darwin (1993, 1994), supplemented by informal morphological groups that were identified in the same manner as *Guettarda* (Valeton, 1909; Wong, 1988).

Special attention was given to including the type species of each genus, and, when possible, a minimum of 2 species were sequenced per genus, subgenus, or informal group. The 42 taxa used in the analysis represent 9 of the 10 core genera of Guettardeae (Table 2), including the type species of 8 currently recognized genera (*Guettarda speciosa*, *Antirhea borbonica*, *Bobea elatior*, *Chomelia spinosa*, *Neolaugeria resinosa*, *Pittoniotis trichantha*, *Stenostomum lucidum*, and *Timonius timon*) and 3 genera currently placed in synonymy, namely, *Dicrobotryum*, *Guettardella*, and *Matthiola* (typified by *Guettarda divaricata*, *Antirhea chinensis*, and *Guettarda scabra*, respectively). Because of a lack of material, *Ottoschmidtia* could not be included, and a single species each was sequenced for *Chomelia* and *Malanea*. For *Antirhea* and *Timonius*, we included 4 and 5 species, respectively, which were selected to represent as much morphological diversity as possible. Three previously published sequences were used for *Neolaugeria densiflora*, *Stenostomum myrtifolium*, and *Timonius nitidus* (Moynihan & Watson, 2001), while 39 new Guettardeae sequences were generated. Two outgroup taxa (*Cuatrecasasiodendron spectabile* and *Gonzalagunia rosea*) were selected from Guettardeae sensu Rova, since they are both placed near to the genera of core Guettardeae in his phylogenies (Rova, 1999).

DNA EXTRACTION

Leaf samples were collected either in silica gel or from herbarium sheets. Genomic DNA was extracted from approximately 1 cm^2 of dried leaf tissue using a modified CTAB methodology. Leaf material was ground in a lysing matrix "A" tube (Qbiogene, Carlsbad, CA) and pulverized for 15 sec. in a Fastprep machine FP-120 (Qbiogene) bead mill at speed 5. Subsequently, 500 μl of Carlson Lysis Buffer (2 g CTAB, 8.18 g NaCl, 0.745 g EDTA, 10 ml 1 M Tris/HCl pH 7.0, nanopure water to 100 ml, verified to pH 9.5, autoclaved, then 1 g PEG 4000 added when cool) and 75 μl of β-mercaptoethanol were added to each tube and incubated at 74°C with occasional shaking for 60–90 min. Following incubation, 575 μl of SEVAG (24 : 1 chloroform : isoamyl alcohol) were added to each tube; the tubes were placed on a tipping board for 30 min. at room temperature, and then centrifuged at 14,000 rpm for 1 min., and ~350 μl of supernatant was removed and added to new tubes containing 1050 μl of NaI solution, 20 μl Glassmilk, and 4 μl TBE modifier (Qbiogene). The tubes were placed on a tipping board for 30 min. at room temperature. Afterward, the tubes were centrifuged at 14,000 rpm for 1 min. and all of the supernatant was discarded. Next, each Glassmilk pellet was washed three times with 800 μl and once with 150 μl of ice cold New Wash solution (Qbiogene). After the final wash, all of the New Wash was aspirated from the Glassmilk pellet and 50 μl of 10 mM Tris-Cl (pH 8.5) elution buffer were added to resuspend the DNA. The tubes were incubated at ~55°C for ~10 min. and then centrifuged for 1 min. at 14,000 rpm. The supernatant containing the DNA was removed and transferred to new tubes and stored at −20°C.

DNA AMPLIFICATION

For DNA amplification, PCR was performed in a 25 μl mixture consisting of 2.5 μl 10× buffer with $MgCl_2$ (Perkin Elmer, Foster City, CA), 9.3 μl autoclaved nanopure water, 2.5 μl BSA (bovine serum albumin), 2.5 μl dNTP, 1 μl each of two 20 μM primers, 5 μl betaine, 0.2 μl Taq polymerase (Qiagen, Valencia, CA), and 1 μl of genomic DNA. All PCR and cycle sequencing reactions were run on a Gene Amp PCR system 9600 (Applied Biosystems, Foster City, CA). The ITS region was amplified using primers NY183 (5′-CCTTATCATTAAGAGGAAGGAG-3′) and NY43 (5′-TATGCTTAAAYTCAGCGGGT-3′), and when necessary two additional internal primers were employed, ITS2 (5′-GCTACGTTCTTCATCGATGC-3′) and ITS3b (5′-GCATCGATGAAGAACGTAGC-3′) (White et al., 1990; Baldwin, 1992; Baum et al., 1998). The PCR conditions for amplification of the ITS region were: 1 cycle of 97°C for 50 sec.; 30 cycles of 97°C for 50 sec., 53°C for 50 sec.; and 1 cycle of 72°C for 1 min. 50 sec., hold 72°C for 7 min., hold at 4°C.

DNA SEQUENCING

To detect successfully amplified products, as well as the possible presence of multiple ITS paralogues of varying length (as discussed by Alvarez & Wendel, 2003) and possible contamination of negative controls, PCR products were examined on 1% agarose gels stained with ethidium bromide and visualized under ultraviolet light. Amplified products were purified with spin columns from the QIAquick PCR purification kit (Qiagen) following protocols provided

Table 2. Species, origin, and voucher information for the 42 ITS sequences used in the present study. Voucher information, with collections italicized, is given for new sequences; literature citation is provided for previously published sequences of three taxa. Herbarium acronyms follow *Index Herbariorum* (Holmgren et al., 1990). Partial sequences are indicated in parentheses following GenBank accession number.

Species	Origin	Voucher information / literature citation	GenBank accession
Antirhea borbonica J. F. Gmel.	Madagascar	*Rakotomalaza 1248* (P)	DQ063666
Antirhea chinensis (Champ. ex Benth.) F. B. Forbes & Hemsl.	China	*K. Y. Tam* s.n., Hong Kong (P)	DQ063702
Antirhea rhamnoides (Baill.) Chaw	New Caledonia	*Achille 688* (P)	DQ063686
Antirhea smithii (Fosberg) Merr. & L. M. Perry	Fiji	*A. C. Smith 7685* (NY)	DQ063667(ITS1)
Bobea elatior Gaudich.	Hawaii	*Motley 2536* (NY)	DQ063668
Bobea sandwicensis (A. Gray) Hillebr.	Hawaii	*Takeuchi 3302* (NY)	DQ063669
Chomelia spinosa Jacq.	Costa Rica	*Seigler 12306* (NY)	DQ063703(ITS1) DQ063704(ITS2)
Cuatrecasasiodendron spectabile Steyerm.	Colombia	*Rova et al. 2093* (GB)	DQ063670
Gonzalagunia rosea Standl.	Costa Rica	*Achille* s.n., Cult. NYBG (P)	DQ063671
Guettarda acreana K. Krause	French Guiana	*Mori 18842* (NY)	DQ063672
Guettarda combsii Urb.	Belize	*Lentz et al. 2853* (NY)	DQ063673
Guettarda crispiflora Vahl	Colombia	*Andersson et al.* 2088 (GB)	DQ063674
Guettarda divaricata (Humb. & Bonpl.) Standl.	Guyana	*Jansen 4908* (NY)	DQ063675
Guettarda elliptica Sw.	Puerto Rico	*Axelrod 3060* (NY)	DQ063676
Guettarda heterosepala Guillaumin	New Caledonia	*Achille 697* (P)	DQ063677
Guettarda hirsuta (Ruiz & Pav.) Pers.	Ecuador	*Delprete 6054* (NY)	DQ063678(ITS1)
Guettarda humboldtensis Guillaumin	New Caledonia	*Achille 672* (P)	DQ063679
Guettarda krugii Urb.	Puerto Rico	*Struwe 1102* (NY)	DQ063680
Guettarda macrosperma Donn. Sm.	Costa Rica	*Hammel 19883* (NY)	DQ063681
Guettarda nannocarpa Urb. & Ekman	West Indies	*Liogier 16631* (NY)	DQ063682
Guettarda noumeana Baill.	New Caledonia	*Achille 662* (P)	DQ063683
Guettarda pohliana Müll. Arg.	Bolivia	*Vee 40536* (NY)	DQ063684
Guettarda pungens Urb.	Puerto Rico	*Grimes 3261* (NY)	DQ063685
Guettarda scabra (L.) Lam.	Puerto Rico	*Acevedo Rodríguez 2840* (NY)	DQ063687
Guettarda sp. "Cuba"	Cuba	*Areces 6538* (NY)	DQ063688
Guettarda speciosa L.	New Caledonia	*Achille 661* (P)	DQ063689
Guettarda splendens Baill.	New Caledonia	*Achille 1010* (P)	DQ063690
Guettarda stenophylla Urb.	West Indies	*Liogier 16950* (NY)	DQ063705(ITS1) DQ063706(ITS2)
Guettarda trimera Guillaumin	New Caledonia	*Achille 870* (P)	DQ063691
Guettarda uruguensis Cham. & Schltdl.	Brazil	*HUCS 12227* (NY)	DQ063692
Malanea macrophylla Bartl. ex Griseb.	Guyana	*Jansen-Jacobs 5396* (NY)	DQ063693
Neolaugeria densiflora (Griseb.) Nicolson	Bahamas	Moynihan & Watson (2001)	AF323055(ITS1) AF323056(ITS2)
Neolaugeria resinosa (Vahl) Nicolson	Puerto Rico	*Taylor & Gereau 10501* (NY)	DQ063694
Pittoniotis trichantha Griseb.	Panama	*Croat 9311* (NY)	DQ063695(ITS1)
Stenostomum acutatum DC.	Puerto Rico	*Axelrod 3288* (NY)	DQ063696
Stenostomum lucidum (Sw.) C. F. Gaertn.	Dominican Republic	*Acevedo Rodríguez 8468* (NY)	DQ063697
Stenostomum myrtifolium Griseb.	Bahamas	Moynihan & Watson (2001)	AF323059(ITS1) AF323060(ITS2)
Timonius densiflorus Valeton	Papua New Guinea	*Takeuchi 8689* (NY)	DQ063698
Timonius flavescens Baker	Malaysia	*Laman et al. 18* (NY)	DQ063699
Timonius nitidus Fern.-Vill.	Guam	Moynihan & Watson (2001)	AF323063(ITS1) AF323064(ITS2)
Timonius polygamus (Forst. f.) Robinson	French Polynesia	*Motley 2044* (NY)	DQ063700
Timonius timon (Spreng.) Merr.	Papua New Guinea	*Motley 2309* (NY)	DQ063701

by the manufacturer. Purified products were cycle sequenced with dye terminator ABI Prism® Ready reaction mix (Applied Biosystems) using dRhodamine or Big Dye v1.0 (1/8 reaction) and 5% dimethyl sulfoxide. Primers for cycle sequencing were the same as those used in the PCRs. Cycle sequencing conditions were: 1 cycle of 95°C for 1 min.; 32 cycles of 96°C for 10 sec., 50°C for 5 sec., 60°C for 3 min.; and hold at 4°C. Products were purified using hydrated Sephadex G-50 DNA Grade F columns (Amersham Pharmacia Biotech, Piscataway, NJ) and dehydrated in a speed vac. The DNA was resuspended in 2.2 μl of formamide (83.5%) and EDTA blue-dextran loading dye (16.5%), heated at 95°C for 2 min., and immediately placed on ice. Sequences were run on a polyacrylamide gel on an ABI Prism 377 DNA sequencer (Applied Biosystems). Gels consisted of 18 g urea ultrapure grade (Amresco, Solon, OH), 0.5 g Amberlite mixed bed resin MB-150 (Sigma-Aldrich, Milwaukee, WI), 27 ml nanopure water, and 5.6 ml Acryl/Bis (Amresco).

Phylogenetic Analysis

Sequences were edited and aligned in Sequencher version 3.1.2 (Gene Codes Corp., Ann Arbor, MI) followed by manual optimization. Gaps were inserted to keep the number of informative characters (indels and substitutions) to a minimum. Indels were treated as unordered, multistate characters; those of equal length that occurred in more than one sequence were considered homologous and scored as separate binary characters added to the data matrix. Insertions that had slightly different sequences in two or more taxa were treated as homologous (Barriel, 1994), and the variable bases within these sequences were then re-coded as new characters (and treated as missing for the taxa in which the insertions were absent). The data matrix is available from the first author.

A heuristic parsimony search was performed using PAUP* version 4.01b (Swofford, 1998), with 100 random addition replicates, TBR branch swapping, and MULPARS option in effect. Relative levels of homoplasy and synapomorphy in the data set were calculated using the consistency index (CI), the retention index (RI), and the rescaled consistency index (RC), as implemented in PAUP*. Internal branch support was estimated with bootstrap analysis (Felsenstein, 1985) using 1000 replicates with TBR branch swapping and simple taxon addition. Pairwise sequence divergence between species of core Guettardeae was calculated with PAUP* ("p" distance, excluding ambiguously aligned sites).

A Bayesian inference of phylogeny (BI) was obtained with the program MrBayes 3.0b4 (Huelsenbeck & Ronquist, 2001) using the GTR+I+Γ model of nucleotide substitution, a general time reversible model that allows (1) a proportion of invariable sites and (2) among-site rate heterogeneity following a gamma distribution. This model was selected as the best fit model for our data from a comparison of 24 models using the Akaike information criterion (Akaike, 1974) as implemented in MrModeltest 2.2 (Nylander, 2004), a modified version of Modeltest 3.6 (Posada & Crandall, 1998). The analysis of the ITS data set (excluding indels) was run using 2×10^6 generations, which were performed on four Markov chains (the temperature of the chains and other parameters were left at default values) with trees sampled every 100 generations. Markov chain convergence occurred rapidly (before 2×10^4 generations), and 2000 trees (2×10^5 generations) were discarded as the "burn-in" of the process. The remaining trees were then used to construct a 50% majority rule consensus tree, which provides estimations of each clade's posterior probability. As a control (Huelsenbeck et al., 2002), four independent searches were run, which yielded similar results. All saved trees from the independent runs ("burn-ins" excluded) were pooled to obtain a consensus tree. Unlike bootstrap support values, posterior probabilities are interpreted as true probabilities for each clade under the assumed model (Rannala & Yang, 1996).

Results

Direct sequencing of the purified PCR products yielded single bands on agarose gels and unambiguous ITS sequences (without obvious multiple bases), showing no evidence of paralogs of varying length. The length of the sequences (including ITS1 + 5.8S + ITS2) ranged from 590 base pairs (bp) (in *Guettarda stenophylla*) to 609 bp (in *Gonzalagunia rosea*). The aligned matrix comprises 680 positions (655 of which represent the aligned sequences and 25 the coding of the indels, including autapomorphies). A total of 84 sites were excluded from the analysis because their alignment was uncertain (most of the indels present among these 84 positions were, however, retained in their recoded form as indicated above). Of these 596 characters included in the analysis, 421 were constant, 76 variable but uninformative, and 99 potentially informative. For two species (*Guettarda hirsuta* and *Pittoniotis trichantha*), ITS2 sequences could not be obtained. *Chomelia spinosa* and *G. stenophylla* could not be sequenced for a region in the 5.8S cistron (17 and 19 bp long, respectively), and the end of ITS2 could not be sequenced for *Timonius flavescens* (46 missing bp). In these cases, the bases were treated as missing data.

The 5.8S cistron is 165 bp in length for all taxa, except in the sequence of *Stenostomum myrtifolium* provided by Moynihan and Watson (2001), which is 2 bp shorter. As often observed (e.g., by Andreasen et al., 1999; Moynihan & Watson, 2001), few mutations occur within this region. The ITS 1 and 2 regions in the 40 species of core Guettardeae included in our sample, range in length from 213 to 223 and 207 to 224 bases, respectively. These lengths fall within the range reported for other angiosperms (Baldwin et al., 1995) and for other groups of Rubiaceae (McDowell & Bremer, 1998; Andreasen et al., 1999; Persson, 2000; Razafimandimbison & Bremer, 2002). Percent pairwise distances between core Guettardeae species range from 0 to 14.2 for ITS 1 (mean = 7.6 ± 2.4), 0 to 13.0 for ITS 2 (mean = 5.3 ± 2.1), and 0 to 9.8 (mean = 5.0 ± 1.5) for the whole ITS region. This amount of ITS variation is comparable to levels usually reported for a single genus (Baldwin et al., 1995), such as *Viburnum* L. (Donoghue & Baldwin, 1993; reviewed in Baldwin et al., 1995) or infrageneric taxa such as *Gilia* sect. *Giliandra* A. Gray (Porter, 1993; reviewed in Baldwin et al., 1995). Compared to other groups of Rubiaceae, variation within core Guettardeae (ca. 500 species) is similar to (or in the case of ITS1, lower than) that reported by McDowell and Bremer (1998) for *Exostema* (Pers.) Rich. ex Humb. & Bonpl. (25 species), and similar to the level observed by Nepokroeff et al. (1999) within the main lineages of tribe Psychotriae, but much lower than for the tribe as a whole (1000 to 1650 species).

The MP analysis yielded 1293 most parsimonious trees, each with a length of 445 (CI = 0.577, RI = 0.695, RC = 0.401). One of the shortest trees is given in Figure 1. The strict consensus (Fig. 2) is well resolved, although numerous clades are not significantly supported in the bootstrap (BS) analysis (BS < 50%). The ingroup node has strong support (BS = 99%) and the topology at the base of the ingroup is fully resolved but poorly supported, in contrast to the terminal branches. Eight pairs of species (*Guettarda divaricata–G. elliptica*, *G. nannocarpa–G. stenophylla*, *G. krugii–G. sp.* "Cuba," *Stenostomum acutatum–S. myrtifolium*, *Bobea elatior–B. sandwicensis*, *G. crispiflora–G. hirsuta*, *Timonius nitidus–T. polygamus*, *Neolaugeria densiflora N. resinosa*) receive high bootstrap support, ranging from 94 to 100%. *Pittoniotis* is sister to the rest of the ingroup, and the remainder of the genera comprise two main clades. The first of these clades contains most species of *Guettarda*, the majority of the Neotropical genera, and the Hawaiian endemic genus *Bobea*. Within this clade, two *Guettarda* species appear isolated as sisters of *Bobea* (comprising the "*Bobea* clade"). The second major clade comprises all the Paleotropical genera, some *Guettarda* species (mostly from New Caledonia), and the West Indian taxa *Neolaugeria* and *Stenostomum* sect. *Stenostomum*. Within this second main clade, a weakly-supported Paleotropical dioecious subclade (BS = 63%) unites all the Paleotropical species included in the analysis except one (*Guettarda speciosa*), while the Neotropical subclades (the first comprising *Neolaugeria* and the second with *Stenostomum* sect. *Stenostomum* + *Guettarda acreana*) are paraphyletic at the base of the clade (no BS support).

Guettarda appears to be polyphyletic in our trees. A majority of the Neotropical taxa sampled are associated with the Paleotropical type species, *G. speciosa*, and thus comprise the "*Guettarda* s. str." clade (BS = 57%). The three remaining species that occur in the New World are isolated (one is associated with *Stenostomum lucidum*, while the other two are part of the *Bobea* Clade) (Fig. 1). All the other *Guettarda* species sampled occur in the Old World and are included within a Paleotropical Dioecious Clade. The complexes of genera usually associated with the three principal members of core Guettardeae (*Guettarda*, *Antirhea*, and *Timonius*) are not evident in our trees. Our limited sampling suggests that *Timonius* and *Bobea* are monophyletic and, although often considered as close relatives, are placed in very distant clades in our trees. *Antirhea* + *Stenostomum* (= *Antirhea* s.l.) is polyphyletic, with *Antirhea* species forming a paraphyletic group with respect to *Timonius* and the New Caledonian *Guettarda* species in the Paleotropical Dioecious Clade, while the members of *Stenostomum* are represented in two additional clades, suggesting it, too, may be polyphyletic.

The BI tree is given in the right half of Figure 2. Its overall topology is quite similar to that of the MP tree and the two analyses essentially recover the same major clades. More clades are well supported in the BI analysis (with posterior probabilities exceeding 0.95) than in the MP analysis (some of which have BS values below 50%), but those clades that are well supported in the MP analysis are likewise in the BI tree. For example, the clade comprising New Caledonian *Guettarda* and 3 *Antirhea* species is strongly supported in the BI analysis (posterior probability, P = 0.99), but unsupported in the MP analysis (BS < 50%), whereas the clade comprising *G. divaricata* and three other Neotropical *Guettarda* species has strong support in both MP and BI analyses (BS = 97%, P = 1.00). The BI tree is slightly less resolved than the MP consensus tree. *Neolaugeria* appears sister to the rest of the ingroup, which forms a polytomy of three clades. The first of these clades encompasses most of the Neotropical genera, including *Guettarda* s. str., *Pittoniotis* and *Malanea* (P = 0.57); the second comprises the *Bobea* Clade (P =

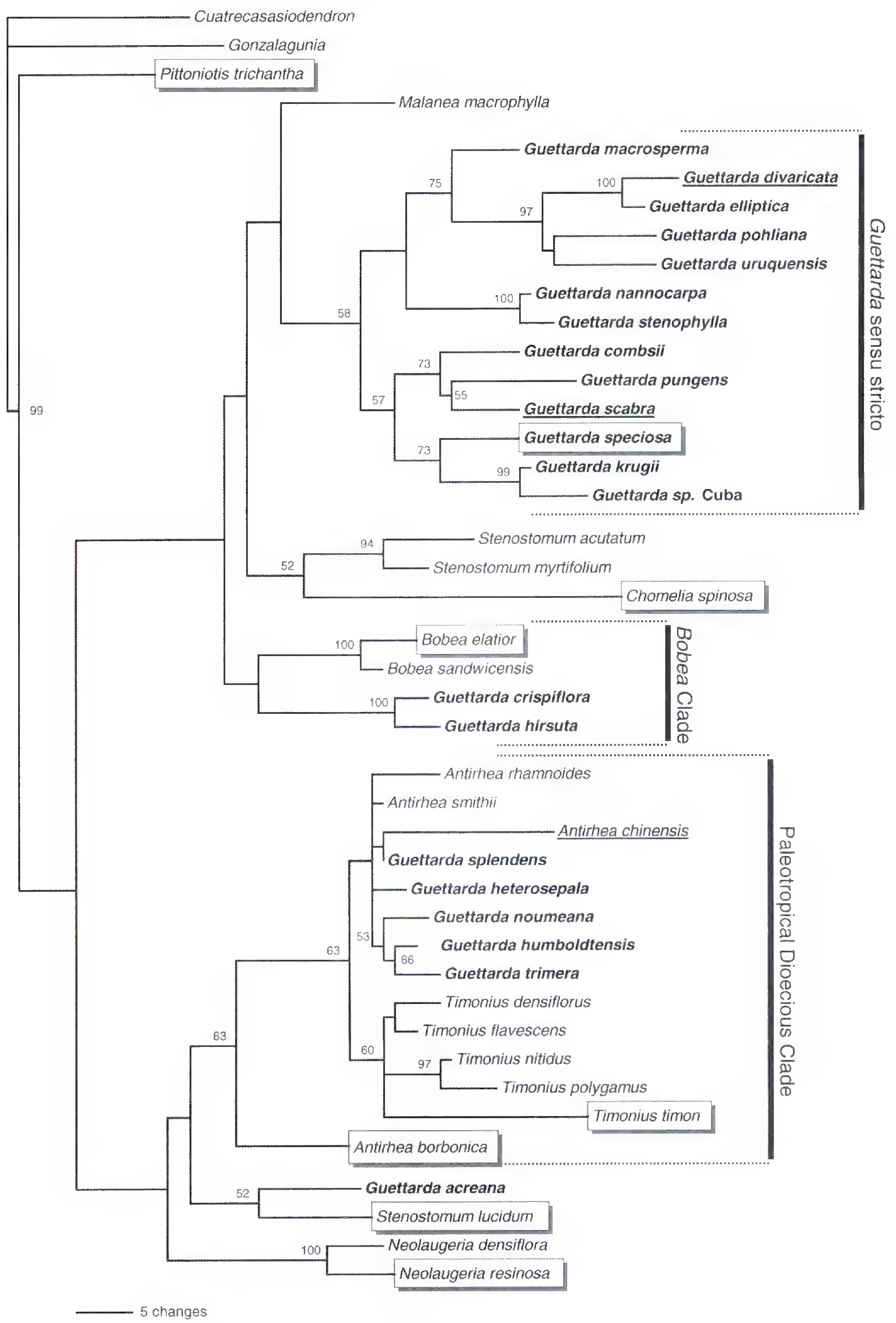

Figure 1. Phylogram of one of the 1293 most parsimonious trees (length = 445; CI = 0.577; RI = 0.695) resulting from the MP analysis of ITS data. Numbers on internodes indicate bootstrap support (in %). *Guettarda* species are in **bold**. Type species of currently recognized genera are placed in a box; type species of genera currently placed in synonymy are underlined (see text for details).

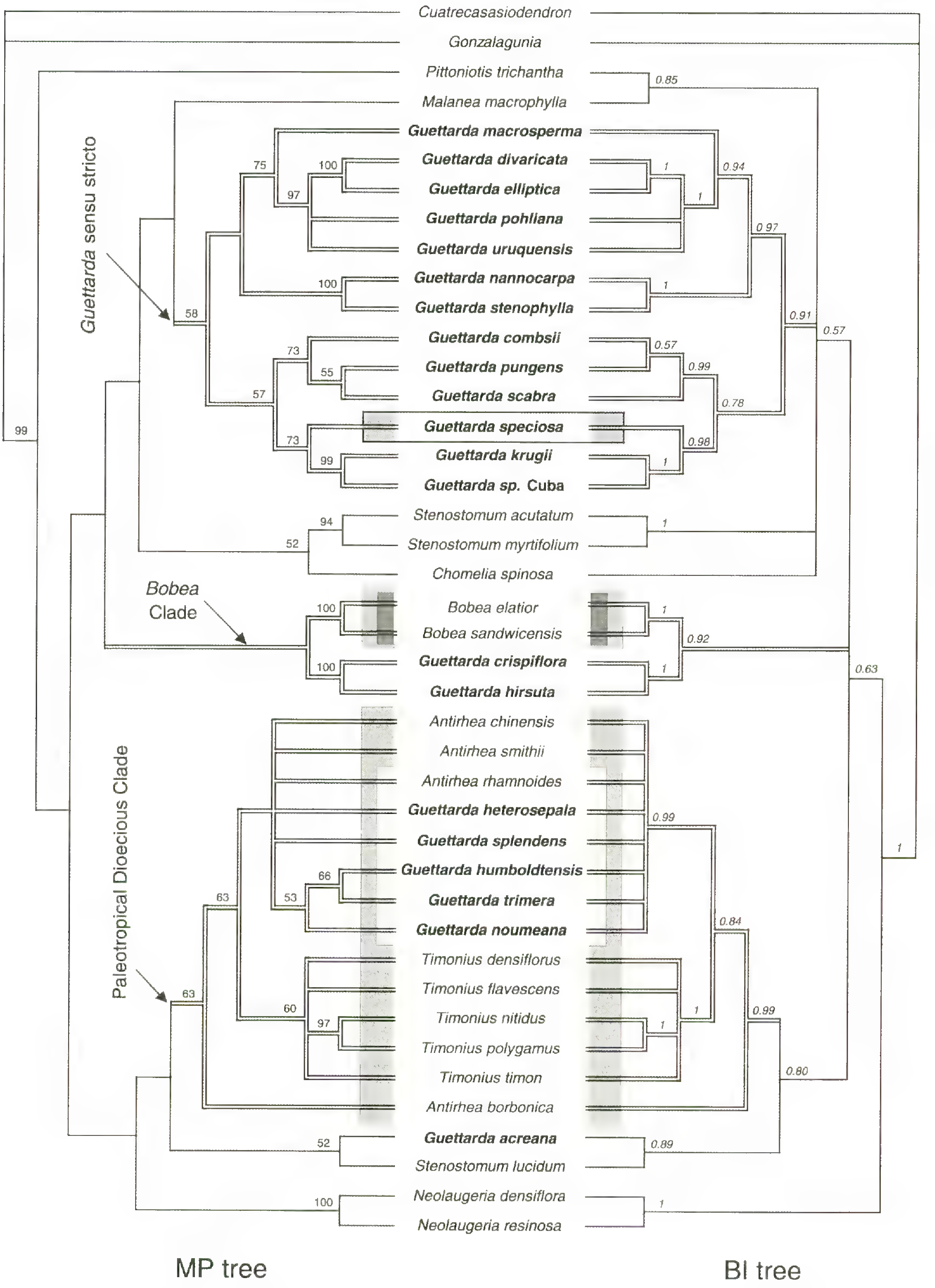

Figure 2. Comparison of the consensus trees from the MP and BI analyses of ITS data. The tree on the left is the strict consensus of 1293 most parsimonious trees (numbers on internodes indicate bootstrap values over 50%). The tree on the right is the 50% majority rule Bayesian consensus tree under the GTR+I+Γ model of substitution from four 2×10^6 generations runs (numbers on internodes indicate posterior probabilities). *Guettarda* species are in **bold**. Clades discussed in the text are indicated by double lines. Geographic distribution of terminal taxa is indicated as follows: gray = paleotropical; dark gray = Hawaii endemic; light gray = endemic to New Caledonia; all others are Neotropical.

0.92); and the third clade (P = 0.80), which is also recovered in the MP analysis, includes the type of *Stenostomum* (*S. lucidum*), *Guettarda acreana*, and the well-supported Paleotropical Dioecious Clade (P = 0.99). Most of the smaller clades recovered in the BI tree are also found in the MP tree, but the position of *Pittoniotis* is inconsistent between the two analyses.

Discussion

The poor support of the larger clades identified in the MP analysis (most with BS < 50% and none exceeding 63%) is unusual as ITS data are generally most informative at suprageneric levels (Baldwin et al., 1995). For example, in a study of Vanguerieae (Lantz et al., 2002), a similar-sized rubiaceous tribe (19 genera, ca. 600 species) that was examined using a comparable data set of 41 ingroup taxa, the major clades are both well-resolved and strongly supported. The situation found in Guettardeae, with low support and/or resolution among the internal nodes, has also been observed in several other groups of Rubiaceae, such as *Alibertia* A. Rich. ex DC. (Persson, 2000) and the Catesbaeeae-Chiococceae complex (Motley et al., 2005), as well as among groups of Asteraceae (Baldwin & Sanderson, 1998; Garcia-Jacas et al., 2001), Fabaceae (Allan & Porter, 2000), and Apiales (Plunkett & Lowry, 2001; Chandler & Plunkett, 2004; Plunkett et al., 2004). This pattern would be consistent with a hypothesized rapid radiation early in a group's evolution, and could explain the lack of support at the base of our trees, which stands in contrast to the morphological diversity that has served to segregate the core genera within the tribe.

Polyphyly of *Guettarda*

Based on our analysis of ITS sequence data, *Guettarda*, as currently circumscribed, is clearly polyphyletic, with species distributed among four distinct clades (Fig. 1). Most of the Neotropical species belong to the first of these, the *Guettarda* s. str. clade (BS = 58%, P = 0.91), which includes the type species, *G. speciosa*, from the Indo-Pacific region. The topology within this clade is well resolved (Fig. 2) even though the species are morphologically quite similar to one another. Members of this group are characterized by usually globose fruits with more than 2 locules, dichasial cymose inflorescences (sometimes reduced to a solitary flower), and a caducous calyx with a circular abscission scar (Fig. 3). These last two characters, although highly distinctive of *Guettarda* s. str., also occur (although not in combination) in three New Caledonian *Guettarda* species, where they may have evolved independently from the core Neotropical lineage: *G. noumeana* and an unnamed close ally (not sampled) have a dichasial cymose inflorescence structure, and a recently discovered undescribed species (not sampled) has a dehiscent calyx with circular abscission.

Within the *Guettarda* s. str. clade, there are three main subclades. The first comprises species from Continental America (BS = 75%, P = 0.94), a few of which, such as *G. elliptica*, extend slightly into the Caribbean Islands. *Guettarda divaricata*, the type species of *Dicrobotryum* Willd. ex Roem. & Schult., is part of this clade. Members of this group are characterized by small- to medium-sized, membranaceous leaves, and possibly also by their pollen (Fig. 2), which is similar to that found in *Antirhea* s. str. (oblate-spheroidal 3-colporate pollen with reticulate exine) (Achille, unpublished data). The second subclade includes two Caribbean species (BS = 100%, P = 1.00), *G. nannocarpa* and *G. stenophylla*, with very small membranaceous leaves, solitary flowers, and small fruits. The third subclade, while weakly supported (BS = 57%, P = 0.78), unites a group of morphologically distinct species mainly from the West Indies along with the Paleotropical *G. speciosa*, the type species. *Guettarda scabra*, the type of *Matthiola* (widely regarded as a generic synonym since Lamarck, 1792), also belongs to this group and closely resembles *G. speciosa*. The fruits of taxa in this third subclade are rather large, as are the leaves, which are often coriaceous or bullate and have scalariform venation. *Guettarda pungens* stands out within this group in having small, spiny leaves, and small fruits. However, all members of the third subclade share a distinct pollen type, characterized by an oblate-spheroidal shape, 3 to 4 pororate apertures, a perforated to reticulate tectum, and short columellae (Achille, unpublished data).

The inclusion of the widely distributed Indo-Pacific species *Guettarda speciosa* in an otherwise strictly Neotropical clade is perhaps best explained by relatively recent long-distance dispersal. *Guettarda speciosa* occurs in strand vegetation and coastal forests on coral limestone, and its fruits have air-filled cavities, making them well adapted to transport by ocean currents. This species is not found in Hawaii or the eastern Pacific, although this may simply reflect the random nature of dispersal. It is perhaps more surprising to note that *G. speciosa* appears to be most closely related to species from the West Indies (such as the widespread coastal species *G. scabra* mentioned above) rather than from the Pacific coast of the Americas, as one might expect.

The second clade containing members of *Guettarda* includes two Neotropical species (*G. crispiflora* and *G. hirsuta*) that are sister in our analysis to *Bobea* (BS <

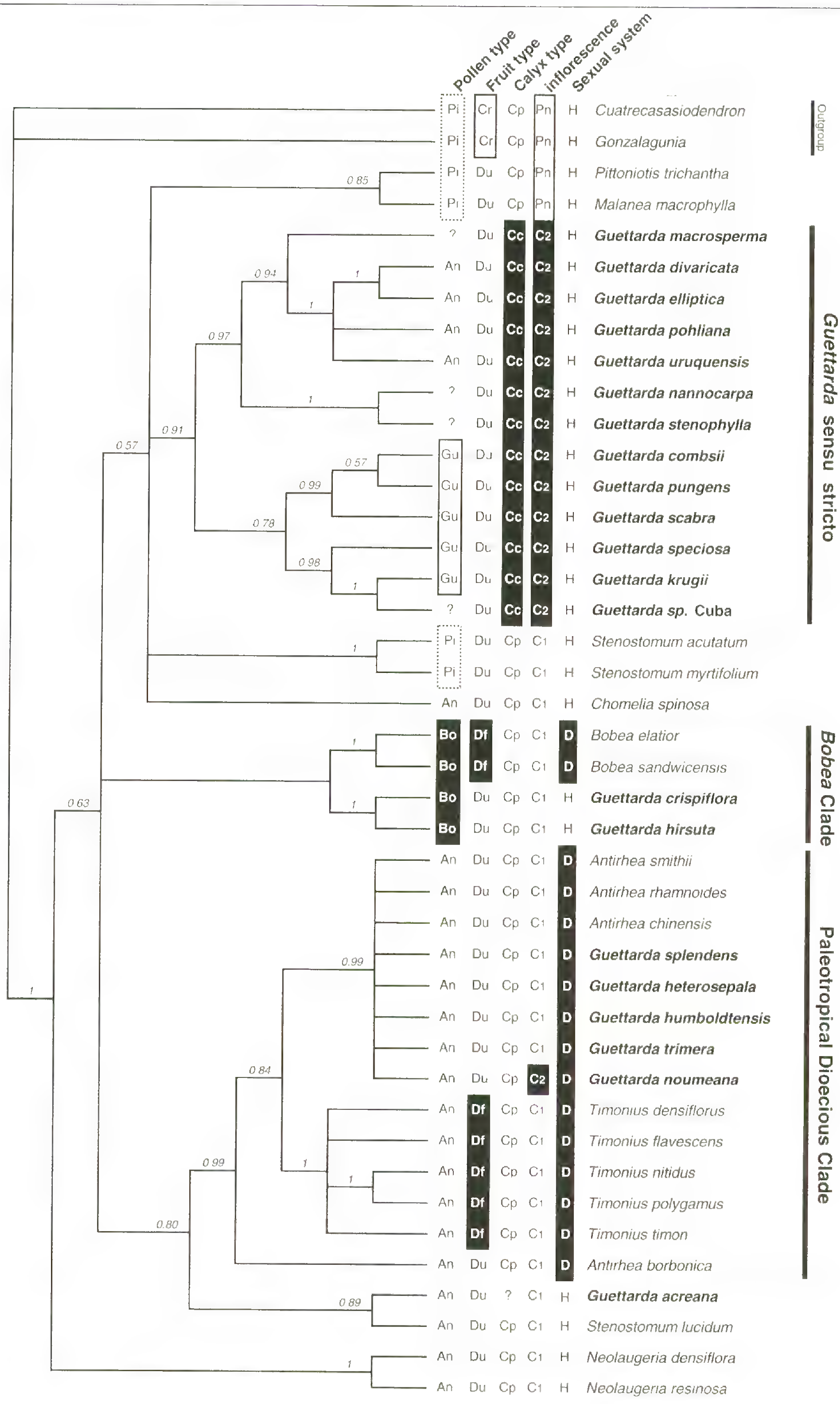

Figure 3. Important morphological characters mapped on the 50% majority rule Bayesian consensus tree. Numbers on internodes indicate posterior probabilities. *Guettarda* species are in **bold**. The symbols indicate the state for each category of characters (Pollen type: Pi = *Pittoniotis*; An = *Antirhea*; Gu = *Guettarda*; Bo = *Bobea*; ? = unknown. Fruit type: Cr = capsular; Du = drupaceous with united pyrenes; Df = drupaceous with free pyrenes. Calyx type: Cc = caducous by abscission; Cp = persistent on fruit; ? = variable. Inflorescence type: Pn = paniculate; C2 = fundamentally dichasial cyme; C1 = fundamentally monochasial cyme. Sexual system: H = hermaphroditism; D = dioecy).

50%, P = 0.92). These taxa exhibit several distinctive characters that separate them from other members of *Guettarda*. Along with a few other apparently closely related species from Central and South America that were not sampled, they form a well-defined group characterized by large stipules with membranaceous margins, scalariform venation, bifid monochasial inflorescences (which differ from the dichasial cymes found in other Neotropical *Guettarda*), small 4-ribbed ovoid fruits with a minute and persistent calyx (see also species descriptions in, e.g., Standley, 1934; Steyermark, 1972; Taylor et al., 2004), as well as "*Bobea* type" pollen (see below under *Bobea*). Although additional molecular data will be required to confirm whether these taxa and *Bobea* are closely related, their distinctive morphological characters suggest that recognition at the generic rank might be in order, in which case the name *Tournefortiopsis* would be available, as it is typified by *T. reticulata* Rusby. (= *Guettarda tournefortiopsis* (Rusby) Standl.), a close relative of *G. crispiflora*.

The *Guettarda* species from New Caledonia constitute a third clade (Fig. 2) that is very well supported in the BI analysis (P = 0.99) although unsupported in the MP analysis (BS < 50%). This clade includes three species of *Antirhea* (*A. chinensis*, *A. rhamnoides*, and *A. smithii*) that would either belong to the segregate genus *Guettardella* according to Jansen (1984) or to *Antirhea* subg. *Guettardella* and *Antirhea* subg. *Mesocarpa* according to Chaw and Darwin (1992). This clade is nested within a broader Paleotropical Dioecious Clade (see below), and is the sister group of *Timonius*. The New Caledonian species of *Guettarda* are morphologically very distinct from the Neotropical members of the genus and from *G. speciosa*. In fact, several characters, including dioecism, a calyx that is almost always persistent in fruit, and monochasial cymes (Fig. 3), are reminiscent of *Antirhea* s.l. The placement of these species within the Paleotropical Dioecious Clade is thus consistent with morphology, and their inclusion in a broadly defined *Guettarda* by Baillon (1879), Guillaumin (1948), and more recently Jaffré et al. (2004) merely reflects an out-of-date concept of the genus that has been abandoned in most other parts of the world. It therefore would seem appropriate to exclude the New Caledonian species from *Guettarda* and transfer them to another genus (see discussion below under *Antirhea*).

It is worth noting that the resolution within the New Caledonian *Guettarda* clade is very weak despite the fact that its members are morphologically quite distinct from one another. Many New Caledonian species of *Guettarda* show one or more characters that are rare or unknown elsewhere in Guettardeae, such as trimerous flowers, corollas with valvate reduplicate aestivation, and a woody endocarp with up to 20 locules. The lack of resolution within this clade reflects a high level of similarity in the ITS sequences of the species sampled. In another study of ca. 20 species from New Caledonia and surrounding areas (Achille & Motley, unpublished), we found that the sequences are identical or differed by only a few bases, suggesting that this clade may comprise a closely related group within which rapid morphological diversification has taken place, perhaps in a manner analogous to that observed within Guettardeae as a whole. The pattern of diversification apparent among the New Caledonian species differs substantially from that of the mostly Neotropical *Guettarda* s. str. clade, where resolution is better and branches are longer (Fig. 1), even though there is comparatively little morphological variability among its members. In order to evaluate a hypothesized radiation centered on New Caledonia, it would first be necessary to sample additional species of *Antirhea* subg. *Guettardella* and subg. *Mesocarpa* (sensu Chaw & Darwin, 1992), the apparent closest relatives of New Caledonia *Guettarda*, according to our results. These subgenera are most diversified in Southeast Asia, but we were able to include only one species from South China (*Antirhea chinensis*), one from Fiji (*A. smithii*), and one from New Caledonia (*A. rhamnoides*).

The fourth group of *Guettarda* identified in our study comprises a single species, *G. acreana*, which appears as sister to *Stenostomum lucidum*. This well known *Guettarda*, widely distributed in northern South America, was sampled in our analysis because of its distinctive morphology, particularly its calyx, which is mostly caducous but not shed by abscission. Its affinities are discussed below under *Stenostomum*.

Our finding of polyphyly in *Guettarda* is consistent with morphological data, as several unique characters are associated with each of the clades revealed in our analysis (Fig. 3). *Guettarda* s. str. can be recognized by its caducous calyx, which appears to be a synapomorphy for the lineage. However, there has been some confusion between what we regard as a truly caducous calyx (shed by abscission) and a calyx that is minute or lost as it disintegrates (without leaving an evident abscission scar), as seen in *G. crispiflora*, which has been misinterpreted by several authors (e.g., Dwyer, 1980; Standley, 1931, 1934; Standley & Williams, 1975; Steyermark, 1974). Species of *Chomelia* have also been reported to possess both a deciduous and persistent calyx (Burger & Taylor, 1993), but additional developmental studies will be required to evaluate whether the nature of the calyx in this genus is homologous with that seen in *Guettarda* s. str. Our

molecular study does not provide any evidence of a close relationship between the type species of *Chomelia* and *Guettarda*, as currently circumscribed, even though, according to Taylor et al. (2004), the morphological distinction between them remains unsatisfactory. With our more thorough sampling, it also appears that the association of *Chomelia* with *G. crispiflora* suggested by Rova et al. (2002) may not reflect a close relationship between the two genera in their stricter sense and thus does not support the inclusion of *Chomelia* within *Guettarda* s. str. (as defined here).

Further analyses will be necessary before extensive nomenclatural changes can be made within *Guettarda* s.l., as most of the larger clades identified in our study are insufficiently supported in the MP bootstrap and BI analyses, and broader sampling is needed for some of them. It would, however, seem appropriate to exclude the New Caledonia species from *Guettarda*, which clearly constitute a group that is distinct from all other members of the genus, as currently circumscribed, and in particular from the type species, *G. speciosa*.

OTHER GENERA OF CORE GUETTARDEAE

Relationships within core Guettardeae, as within *Guettarda*, appear well correlated with geography. All the Paleotropical species sampled, except the Hawaiian taxa and the widespread coastal species *G. speciosa*, belong to a Paleotropical Dioecious Clade that is well supported in the BI analysis ($P = 0.99$; Fig. 2). Since the closest allies of the genera comprising core Guettardeae are Neotropical (Bremer, 1996; Bremer & Thulin, 1998; Rova et al., 2002), this suggests a New World origin for the group, with presumably two separate events involving dispersal (or vicariance) to account for the presence in the Old World of the Paleotropical Dioecious Clade and of *G. speciosa*. Dioecy characterizes all members of the Paleotropical Dioecious Clade, viz. *Timonius*, *Antirhea* and the New Caledonian *Guettarda* species, in contrast to other core Guettardeae, whose sexual system is almost always hermaphroditism, the only exception being the dioecious Hawaiian endemic genus *Bobea* (cited as polygamodioecious by Darwin & Chaw, 1990).

Timonius. Despite the presence of considerable morphological heterogeneity within *Timonius* (Wong, 1988), this genus is easily distinguished among Paleotropical Guettardeae by its free pyrenes. The five species included in our sample form a clade that is well supported in the BI analysis ($P = 1.00$), but only weakly so in the MP analysis (BS = 60%). The notion that *Timonius* is related to the endemic Hawaiian genus *Bobea* is not confirmed by our results, despite the fact that they are both dioecious, a character found throughout the Paleotropical clade, and that they share free pyrenes, which are not known anywhere else in the tribe. *Timonius* is further distinctive among Rubiaceae because of its large number of ovary locules, which can exceed 500 in some species (Darwin, 1994), whereas most members of the family have bilocular ovaries. However, several other groups also show increases (albeit much more modest) in locule number, including some Neotropical *Guettarda*, *Bobea*, and most members of the Paleotropical Dioecious Clade. Thus, although characters of the gynoecium are usually considered among the most important in infrafamilial classification of Rubiaceae, it seems very likely that an increase in the number of locules has occurred several times independently within Guettardeae, although the evolution of this character within the tribe may not be strictly homologous in the lineages in which it occurs.

Antirhea. Although numerous genera and species have been associated with or included in *Antirhea*, our data suggest that a restricted generic circumscription may be appropriate. The monotypic Neotropical genus *Pittoniotis* has sometimes been included in *Antirhea* (e.g., by Dwyer, 1980), but neither of our trees provides evidence for a close relationship with either *Antirhea* or the previously included Neotropical segregate genus *Stenostomum* (Fig. 2). The morphological basis traditionally invoked for this putative relationship is rather weak, essentially limited to the presence in both *Pittoniotis* and *Antirhea* of calyx-crowned drupes with few united pyrenes, characters that are in fact fairly common within core Guettardeae. *Pittoniotis* differs, however, in several important ways, such as having paniculate inflorescences, exserted stamens, and distinctive prolate 3-colporate pollen with perforate exine (the latter feature occuring also in *Stenostomum* sect. *Resinanthus* Borhidi, represented in our analysis by *S. acutatum* and *S. myrtifolium*), whereas *Antirhea* has monochasial cymes, included stamens, and oblate-spheroidal 3-colporate pollen with reticulate exine (Achille, unpublished data). All the distinctive features of *Pittoniotis* mentioned above are shared with *Malanea* (Fig. 3), but occur nowhere else within core Guettardeae (the outgroup taxa used in this study, however, exhibit some of them: Achille, pers. obs.). This suggests an affinity between *Pittoniotis* and *Malanea* that would be congruent with the sister relationship indicated by the BI analysis ($P = 0.85$).

The ITS data clearly indicate that *Antirhea* s.l. (i.e., including *Stenostomum*) is polyphyletic. Even the

more restricted definition of the genus proposed by Chaw and Darwin (1992), who included only the Paleotropical species but excluded *Stenostomum*, appears to be paraphyletic with respect to Paleotropical members of *Guettarda* and *Timonius*. Our sampling, while modest, suggests that in order to render *Antirhea* sensu Chaw and Darwin (1992) monophyletic, it would be necessary to include both *Timonius* and the New Caledonia species of *Guettarda*. If such a broad definition were used, *Antirhea* would constitute a very large genus (comprising about 230 species) that corresponds more or less to Schlechter's (1906) broad concept of *Timonius*. Adopting such a circumscription would, however, make it very difficult to define *Antirhea* based on morphological characters and thus does not seem advisable.

It would therefore seem best to limit *Antirhea* to species from the Indian Ocean, comprising *A. borbonica* (the type species) and two close relatives (*A. bifurcata* (Desf.) Hook. and *A. madagascariensis* Chaw), which together correspond to *Antirhea* sensu Jansen (1984), or *Antirhea* subg. *Antirhea* sensu Chaw and Darwin (1992). In our analysis, this group (represented by *A. borbonica* only) is sister to all the other Paleotropical Guettardeae (BS = 63%, P = 0.99). A more narrowly defined *Antirhea* would be easily characterized by its monomorphic male and female inflorescences (i.e., which have similar branching patterns), ovaries with only 2 or 3(4) locules, and the presence of crystals in the leaf epidermis.

If this narrower interpretation of *Antirhea* is adopted, a new generic placement would be needed for the species belonging to *Antirhea* subg. *Guettardella* (represented in our study by *A. chinensis*, the type species of *Guettardella*, and by *A. rhamnoides*) and *Antirhea* subg. *Mesocarpa* (represented by *A. smithii*). Chaw and Darwin (1992) recognized both these subgenera, which together formed a clade in their analysis. The first subgenus comprises species mostly from Malesia, Southeast Asia, and the southwest Pacific with small, 3- to 11-locular fruits, and the second includes Melanesian species with large, 8- to 16-locular fruits. Taken together, this group corresponds to *Guettardella* sensu Jansen (1984), which could be resurrected to accommodate these taxa. As the New Caledonian species of *Guettarda* may belong to the same broad clade as the *Guettardella* group (BS < 50%, P = 0.99), they could perhaps also be included in an even more broadly defined *Guettardella*. If this relationship is confirmed by future studies and a substantially enlarged *Guettardella* is recognized, it would, however, constitute a heterogeneous group, since the New Caledonian species are morphologically quite variable and different from those currently included in *Guettardella*.

Stenostomum. Our results suggest that *Stenostomum* may also be polyphyletic, with *S. lucidum* in a weakly supported sister relationship to *Guettarda acreana* (BS = 52%, P = 0.89) and two other species (*S. acutatum* and *S. myrtifolium*) forming a separate clade (BS = 94%, P = 1.00) that is sister to *Chomelia* in the MP analysis (BS = 52%). As mentioned above, Borhidi and Fernandez (1993–1994) placed *S. lucidum* in *Stenostomum* sect. *Stenostomum*, whereas the other two species in our sample belong to their section *Resinanthus*. Our study supports the idea that these two groups are distinct, as suggested by morphology (Borhidi & Fernandez, 1993–1994), but their placement in different parts of our trees would not be consistent with maintaining them as a single genus. The possible sister relationship of *G. acreana* to the type species of *Stenostomum*, although weakly supported in our trees, would on the other hand be consistent with morphology, as several characters shared between these taxa (e.g., similar inflorescence structure, small ovoid fruits, and a calyx that is not shed by abscission) are not found in members of *Guettarda* s. str. For example, Bremekamp (1959), who was familiar with *Stenostomum* (under the name *Antirhea*) in Central America and the West Indies, while studying an undetermined specimen of *G. acreana* collected in Surinam, recognized it as an *Antirhea*. He consequently did not suspect any relation of his specimen to *Guettarda* and described it as a new species, *A. surinamensis* Bremek. It might thus prove appropriate to include the South American *G. acreana* within *Stenostomum*, a relationship that earlier authors (e.g., Steyermark, 1972) perhaps overlooked simply because *Stenostomum* occurs farther to the north, from the West Indies to northern Central America (Borhidi & Fernandez, 1993–1994).

Despite being well distinguished by having stipules united into a sheath, *Neolaugeria* was merged into *Stenostomum* (as a third section) by Borhidi and Fernandez (1993–1994). We are unable to confirm this interpretation, as the two species of *Neolaugeria* in our sample (which comprise a well supported pair, BS = 100%, P = 1.00) form a paraphyletic group with the *S. lucidum* clade in the MP tree, whereas they appear as sister to the rest of the ingroup in the BI tree, although both topologies are unsupported (BS < 50%, P = 0.63). Moynihan and Watson (2001) also rejected the inclusion of *Neolaugeria* in *Stenostomum* using ITS sequence data. Their results were, however, based on an analysis that included only one species of *Stenostomum*, *S. myrtifolium*, a member of section

Resinanthus, which in our study was resolved in a clade distant from the *Neolaugeria* group.

Stenostomum has been considered a synonym of *Antirhea* by some authors (e.g., Schumann, 1891; Standley, 1934; Bremekamp, 1966; Airy Shaw, 1973; Steyermark, 1974; Robbrecht, 1988) because these two genera are morphologically similar in several aspects (e.g., monochasial cymes, a stony endocarp often with few locules, and a persistent calyx). Our results suggest that the type species of *Stenostomum* is indeed closely related to *Antirhea*, and in particular to *A. borbonica* (the type of that genus), although placed sister to the Paleotropical clade. Our data are thus consistent with Chaw and Darwin's (1992) suggestion that *Stenostomum* is best treated as a distinct genus.

Bobea. The exclusion of the Hawaiian genus *Bobea* from Guettardeae was proposed by Rova (1999), but both our analyses suggest that *Bobea* is nested well within the tribe (BS = 99% and P = 1.00). Furthermore, the placement of *Bobea* within core Guettardeae has long been recognized based on morphological features. *Bobea* has numerous characters in common with other genera of core Guettardeae, including typically secund, monochasial inflorescences that are once-dichotomous at the base; fleshy fruits with numerous similarly-structured pyrenes; elongate cylindrical seeds with small cotyledons and topped by an obturator; and overall vegetative and floral morphology which closely resembles some species of *Antirhea*, *Guettarda*, and *Timonius*. The position of *Bobea* in the tree presented by Rova (1999) thus seems at odds with both ITS data and morphology, suggesting that Rova's placement may have resulted from an error in sampling or analysis.

Within core Guettardeae, *Bobea* does not appear to be closely related to *Timonius*, despite the fact that these two genera were once considered as synonyms (Candolle, 1830) or, more recently, as close allies (Darwin & Chaw, 1990). On the contrary, as indicated earlier, *Bobea* may instead be sister to *G. crispiflora* + *G. hirsuta*, thus forming the *Bobea* Clade, although this relationship is weakly supported in the BI analysis (P = 0.92) and unsupported in the MP tree (Fig. 2). It is worth noting, however, that all of these species are well-characterized (Fig. 3) by the presence of "*Bobea* type" pollen (spheroidal porate pollen with very thick, reticulate exine; Achille, unpublished data), which appears to be unique in the tribe, and also by their inflorescence structure (bifid monochasial cymes), distinctive from *Guettarda* s. str. A New World origin of *Bobea* may thus be plausible, since *G. crispiflora* and its relatives are distributed in the Neotropics and in particular on the Pacific coast of Central and South America and the Cocos Islands, rather than a western Pacific origin, as implied by a traditionally assumed relationship to the Paleotropical *Timonius*. If *Bobea* is indeed derived from a Neotropical ancestor, its dioecy may have evolved independently from the Paleotropical Dioecious Clade, perhaps as an adaptation to an insular environment, a pattern that is seen in many other Hawaiian groups (Sakai et al., 1995). Hawaii has one of the highest incidences of dioecy (14.7%) of any flora in the world, and many dioecious lineages are derived from dimorphic ancestors, which was thought to be the case for *Bobea* (Sakai et al., 1995). *Bobea* may thus be a 13th Hawaiian lineage that is believed to have evolved dioecy from hermaphroditic colonists (Sakai et al., 1995).

Conclusions

Our study, using a broad sampling that represents most of the morphological and geographical diversity within *Guettarda*, indicates that the genus is polyphyletic. *Guettarda* should probably be restricted to a group of species characterized by dichasial cymes (sometimes reduced to solitary flowers) and a caducous calyx with a circular abscission zone, which is well-diversified in the Neotropics, but also comprises a single widespread species in the Paleotropics. The numerous endemic New Caledonian species currently assigned to *Guettarda* clearly belong to a distinct *Antirhea-Guettardella* complex, whose internal relationships are in need of further study. Our results also indicate that several morphologically distinctive Neotropical species traditionally included in *Guettarda* are placed outside *Guettarda* s. str., although their exact affinities remain unclear.

Our study also provides some interesting insights concerning the delimitations of other genera in core Guettardeae and the distribution of characters within the tribe. Our data confirm that the Neotropical genus *Stenostomum* is distinct from *Antirhea*, which should thus be considered as strictly limited to the Old World. Furthermore, *Antirhea* and *Stenostomum* both appear to be polyphyletic and may thus require the application of narrowed generic circumscriptions. Features of the gynoecium (such as the number of locules and fusion of the pyrenes), which have often been considered among the most important characters for recognizing suprageneric taxa within Rubiaceae, do not appear to be particularly well correlated with the groups identified in our analysis. Several interesting correlations have, however, been found between our phylogeny based on ITS data and the distribution of certain previously-ignored or underutilized characters. For example, a large Paleotropical

Dioecious Clade is characterized by its distinctive sexual system. The recognition of several pollen types among the members of core Guettardeae, and the homogeneity in pollen type seen within several clades identified in our phylogeny, also suggest that palynological characters may be valuable for further studies at the generic and/or specific levels within the tribe. Finally, with regard to biogeography, although *Guettarda* s.l. and *Antirhea* s.l. have generally been considered to show trans-Pacific distributions with two disjunct areas of diversification, one in the Old World and another in the Neotropics, our study suggests that this interpretation was erroneously based on non-monophyletic generic concepts.

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A SYSTEMATIC REVISION OF *CAPPARIS* SECTION *CAPPARIS* (CAPPARACEAE)[1, 2]

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Abstract

A systematic revision of *Capparis* sect. *Capparis*, from western and Central Asia, North Africa, and Europe, is presented here. The taxonomy of this section has been approached combining morphological, biogeographical and molecular data when available. Ten species are recognized, including two new species, *Capparis atlantica* and *C. zoharyi*. In addition, four new subspecies are presented: *Capparis ovata* subsp. *myrtifolia*, *C. parviflora* subsp. *sphaerocarpa*, *C. sicula* subsp. *mesopotamica*, and *C. sicula* subsp. *sindiana*. Lectotypes are designated for *C. aegyptia*, *C. hereroensis*, *C. mucronifolia*, *C. elliptica*, *C. mucronifolia* Boiss. subsp. *rosanoviana*, *C. rupestris*, *C. ovata*, *C. parviflora*, *C. spinosa* var. *canescens*, *C. sicula* subsp. *herbacea*, and *C. sicula* subsp. *leucophylla*. A full taxonomic treatment, keys, and distribution maps of the recognized species are provided. The two new species are illustrated.

Key words: Capparaceae, *Capparis*, taxonomy.

Capparis (Καππαρις) is a name coined by Theophrastus (4th century BC) and endorsed by Dioscorides (1st century AD). It seems to have come into wide use after the spread of the Arab culture in the Middle Ages. The Genus *Capparis* was created by Linnaeus (1753, 1754) with the description of *Capparis spinosa* L. and other *Capparis* species (Jarvis et al., 1993). *Capparis* comprises around 250 species distributed in tropical and subtropical zones of southern America, Europe, Africa, Madagascar, Asia, Australia, and the Pacific Islands (Willis, 1988).

Taxonomic History

Candolle (1824), who proposed a sectional division of the genus, provided the first comprehensive systematic approach to *Capparis*. Old World taxa belong to Section 1. *Capparis* (= *Eucapparis* DC.). Representative species: *C. spinosa* L. with four subsections. Subsection *Capparis* (= *Pedicellares* DC.). Flowers always solitary at leaf axils. In addition to *C. spinosa* and related species, other representatives include species such as *C. cartilaginea* Decne. Some species with geminate flowers or in bunches of three, rarely alone, such as *C. horrida* L. f., *C. pubiflora* DC., and *C. canescens* DC., were later transferred to section *Monostichocalyx* Radlk. and section *Busbeckea* (Endl.) Benth. & Hook. Subsection *Seriales* DC. Racemose inflorescences or in series on the stems. Representative species: *C. zeylanica* L., *C. acuminata* Willd., *C. quadriflora* DC., *C. rotundifolia* Rottl., *C. brevispina* DC. Subsection *Corymbosae* DC. Corymbose inflorescences. Representative species: *C. sepiaria* L., *C. umbellata* Brown ex DC., *C. incanescens* DC. subsection *Octandrae* DC. Flowers with 8 stamens. Representative species: *C. racemulosa* DC., *C. oleoides* Burch., *C. coriacea* Burch.

New World taxa are included in five sections. Section 2. *Capparidastrum* DC. Stems generally thorny, oval sepals without gland, and short gynophore. Representative species: *C. brasiliana* DC., *C. macrophylla* HBK, *C. cuneata* DC. Section 3. *Cynophalla* DC. Stems generally thorny, oval sepals possessing basal gland or foveola, and large gynophore. Representative species: *C. cynophallophora* L., *C. guayaquilensis* HBK, *C. amplissima* Lam. Section 4. *Calanthea* DC. Rounded fruit section, thin sepals, linear, and sharp. Representative species: *C. nemorosa* Jacq., *C. pulcherrima* Jacq. Section 5. *Breyniastrum* DC. Triangular sepals, sharp; always very short gynophore. Representative species: *C. ferruginea* L., *C. incana* HBK, *C. indica* (L.) Rawc. & Rendle.

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Section 6. *Quadrella* DC. Angular fruit section. Representative species: *C. jamaicensis* Jacq., *C. intermedia* HBK, *C. crotonoides* HBK. The species *C. decidua* (Forssk.) Edgew. with deciduous leaves, up to 20 × 3 mm in size, is included by Candolle (1824) in the genus *Sodada* Forssk.

This was followed in part by Bentham & Hooker (1862), although they created three new sections: section *Sodada* (Forssk.) Benth. & Hook. including *C. decidua*; section *Busbeckea* (Endl.) Benth. & Hook. including Australian species; and section *Beautempsia* (Gaud.) Benth. & Hook. including one American species.

Zohary (1960) proposed new systematics based on a partial geographical review of this genus restricted to the Mediterranean region and West Asia. He recognized two biogeographical groups: the tropical, including *Capparis decidua*, *C. cartilaginea*, *C. mucronifolia* Boiss., and the Mediterranean, including species that have lost their links with the tropical African stock (*C. spinosa*, *C. sicula* Veill., *C. leucophylla* DC.). All species belong to section *Capparis* in the sense of Candolle (1824).

Jacobs (1965) attended to the *Capparis* species from India to the Pacific, and organized them into four sections: 1. section *Capparis*, monotypic with *C. spinosa*, s.l.; 2. section *Sodada*, monotypic with *C. decidua*; 3. section *Monostichocalyx* Radlk., in a new circumscription containing most of the species formerly included in section *Capparis* (= *Eucapparis* DC.), with about 65 species in the area under revision; 4. section *Busbeckea*, with 14 species in all.

Higton and Akeroyd (1991) reviewed the diversity of *Capparis* in the Mediterranean region, especially in connection with *C. spinosa*, examining six species in one section, which were finally reduced to a single species with two subspecies.

Hall et al. (2002) analyzed sequence variation for a large sampling of Brassicaceae and Capparaceae, using two chloroplast regions, *trn*L-*trn*F and *ndh*F. The results of parsimony and likelihood analyses strongly supported the monophyly of Brassicaceae plus Capparaceae and recognized three clades: Capparaceae subfamily Capparoideae, subfamily Cleomoideae, and Brassicaceae. Habit and fruit characteristics demarcate these three clades. All Capparoideae are woody, which is the plesiomorphic condition for the Brassicaceae and Capparaceae clades. The herbaceous habit is generally found in Cleomoideae and Brassicaceae. Indehiscent, fleshy fruits are plesiomorphic in Capparaceae and Brassicaceae and are the dominant fruit type of Capparoideae. Brassicaceae and Cleomoideae both have dehiscent capsules with a replum, a synapomorphy shared by these two clades. The dehiscent fruits of Capparoideae are almost always fleshy in nature in contrast to the often dry fruits of Cleomoideae and Brassicaceae. Floral symmetry, stamen number, leaf type, and fruit type all show homoplasy. Clades within Capparoideae show a biogeographical pattern based on this sampling with a New World clade (all New World representatives of *Capparis*, *Belencita* Karst., *Morisonia* L., *Boscia* Lam., and *Cadaba* Forssk.) and an Old World clade (*Maerua* Forssk., *Tylachium* Lour., *Ritchiea* R. Br., and *Cadaba*). The Old World species *Capparis tomentosa* Lam. is nested within an otherwise New World clade (based only on *trn*L-*trn*F). Old World *Capparis spinosa*, the type of genus *Capparis*, is nested within an Australasian clade, with *Apophyllum anomalum* F. Muell. (western New South Wales) and *Capparis callophylla* Blume (Java) (based only on *trn*L-*trn*F).

DNA sequencing of the chloroplast *rcb*L gene nested New World *Capparis hastata* Jacq. and Old World *C. sandwichiana* DC. in the same clade, but sampling was restricted to these two *Capparis* species and comparison was made with *Crataeva* L. species (Rodman et al., 1998; Cummings et al., 2003).

Taxonomic confusion of *Capparis* sect. *Capparis* is reflected in the number of combinations and changes of rank, with frequent placement under *C. spinosa* (Zohary, 1960; Jacobs, 1965; Higton & Akeroyd, 1991). *Capparis spinosa* has become a blanket identification used to cover the scarce level of definition of the taxa in *Capparis* sect. *Capparis* (Greuter et al., 1984). This has both taxonomic and economic implications, as *Capparis* flower buds are the crude material used as commercial capers and variability in this economic product is determined mostly by taxonomic differences (Inocencio, 2001; Inocencio et al., 2002). Molecular studies of *Capparis* sect. *Capparis* have been scarce or restricted to small sampling (Fici, 2001).

A genetic fingerprinting technique (AFLP) was used by Inocencio et al. (2005) to examine the relationships among *Capparis* species. Genetic distances, based on AFLP data, were estimated for 45 accessions of *Capparis* species from Spain, Morocco, and Syria. The results of this analysis support the differentiation of four (*C. orientalis* Veill., *C. sicula*, *C. aegyptia* Lam., and *C. ovata* Desf.) of the five taxa sampled. The fifth, excluded, species was *C. spinosa*. The group of plants recognized as *C. spinosa* on the basis of morphological characters such as shrub procumbent or somewhat erect, stipules usually weak or vestigial, rarely strong, very long and thin (0.3–0.6 cm long), indument on leaves always very lax, and trichomes thick and long (300–500 μm long), is found almost exclusively in cultivation. Several cultivars of *C. spinosa* appear in an intermediate position between

C. orientalis and *C. sicula* and overlap with *C. orientalis*. The other two species, *C. aegyptia* and *C. ovata*, are morphologically distinct, characterized by their habit, stipules, and leaves (*C. aegyptia*: shrubs somewhat erect; twigs gray-green or blue-green with waxy cover; stipules curved, retrorse; leaves obovate to ovate, bases and apices rounded, 2–3 × 1.8–3 cm; *C. ovata*: shrub pendulous; adult leaves ovate, texture subcoriaceous; stipules curved, mostly antrorse).

The objective of the present revision is to provide a general taxonomy, based fundamentally on morphological data for *Capparis* sect. *Capparis*.

Taxonomic Context of *Capparis* sect. *Capparis*

Capparis belongs to the subfamily Capparoideae (Capparaceae), that also includes *Cadaba*, *Crataeva*, *Morisonia*, *Boscia*, and other New World and Old World genera (Hall et al., 2002). The different genera overlap in molecular studies (Hall et al., 2002), although a marked biogeographical distinction is found between New World and Old World groups, recognized at the level of section or subsection (Candolle, 1824; Bentham & Hooker, 1862; Hall et al., 2002). A tentative infrageneric division is presented in Table 1 in order to contextualize *Capparis* sect. *Capparis*. There are many unresolved taxonomic and nomenclatural issues for infrastructure in *Capparis*. Therefore taxa in Table 1 are merely presented as a synthesis of major groups.

Geographic Distribution and Endemism

Capparis is mostly a Pantropical genus, but section *Capparis* is almost strictly Holarctic with six exclusive species (*C. aegyptia*, *C. atlantica* Inocencio, D. Rivera, Obón & Alcaraz, sp. nov., *C. orientalis*, *C. ovata*, *C. spinosa*, *C. zoharyi* Inocencio, D. Rivera, Obón & Alcaraz, sp. nov.), one paleotropical species (*C. hereroensis* Schinz), and three in holarctic and paleotropical areas (*C. mucronifolia*, *C. parviflora* Boiss., *C. sicula*). Here we name the floristic categories (kingdoms and regions) according to Takhtajan (1986). *Capparis* sect. *Capparis* has its maximum diversity in the Mediterranean Region (Holarctic) with seven species (*C. aegyptia*, *C. atlantica*, *C. orientalis*, *C. ovata*, *C. spinosa*, *C. zoharyi*, *C. sicula*). It is followed next by the Saharo-Arabian Region (also Holarctic) with six species in North Africa and the Arabian Peninsula (*C. aegyptia*, *C. ovata*, *C. zoharyi*, *C. mucronifolia*, *C. parviflora*, *C. sicula*). The Irano-Turanian Region (Holarctic) is inhabited by four species extending along most of West and Central Asia (*C. aegyptia*, *C. mucronifolia*, *C. parviflora*, *C. sicula*). The Sudano-Zambezian Region (Paleotropical) is inhabited by three species in tropical East Africa, littoral Arabia, western India, and southern Pakistan (*C. mucronifolia*, *C. parviflora*, *C. sicula*). The African Karoo-Namib and Indian regions are inhabited by one single species each (*C. hereroensis* and *C. sicula*, respectively). *Capparis sicula* is the most widespread species, stretching from the Western Mediterranean to the Himalayan Mountains and the Rajasthan of India (Indian Region, Paleotropical). *Capparis hereroensis*, in western Namibia, is the only species confined to the African Karoo-Namib Region (sensu Takhtajan, 1986). Endemic taxa are infrequent in this section, although *C. atlantica* is endemic to the Atlas range in Morocco, *C. mucronifolia* Boiss. subsp. *rosanoviana* (B. Fedtsch.) Inocencio, D. Rivera, Obón & Alcaraz is endemic to central Tajikistan, and *C. parviflora* Boiss. subsp. *sphaerocarpa* Inocencio, D. Rivera, Obón & Alcaraz is endemic to the western provinces (Nimruz, Farah, Herat) in Afghanistan.

Economic Importance

Species of *Capparis* sect. *Capparis* are widely used as food and medicine in the Old World. *Capparis spinosa* is almost exclusively known in cultivation. The supposed wild individuals of *C. spinosa* are often remnants of ancient caper fields or escaped from cultivation. Local caper cultivars and ethnovarieties are recognized throughout the Western and central Mediterranean region (Spain, France, Italy, continental and insular). These principally belong to *C. spinosa*, but also to *C. orientalis* (Rivera et al., 1999, 2003b). Flower buds, consumed as brined product, are a rich source of the antioxidant phenolic compound rutin (Inocencio et al., 2000). The use of *Capparis* species by humans has been traced to the Prehistory and early historic times of Western Europe (1st–2nd cent. A.D., Tongeren, Belgium), the Mediterranean region (9000–7400 B.C., Franchti Cave, Greece), and West Asia (9th–8th mill. B.C., Tell Mureybit, Syria), as evidenced by the presence of these species in archaeological sites (Rivera et al., 2002).

Material and Methods

The herbaria and libraries of the following institutions were consulted: BM, E, JEPS, K, MA, MUB, OXF, P, RSA, and UMH. Specimens on loan were received from BISH, BR C, G, HUB, HUJ, MARSSJ, RNG, and US. Special collection trips were conducted in North Africa, western Asia, and Mediterranean Spain to obtain fresh material for molecular studies, for the in vivo study of floral characters, and for

Table 1. Tentative infrageneric division of *Capparis* presented in order to contextualize *Capparis* section *Capparis*.

Infrageneric rank	Characters	Representative species	Distribution
Sect. *Breyniastrum* (Plum.) DC.	Branches unarmed. Leaves large (more than 0.3 cm wide) and persistent. Flowers in simple or compound inflorescences (racemes, umbels, corymbs), although solitary flowers at the leaf axil may appear in some individuals. Sepals triangular, sharp; gynophore always very short. Flowers with numerous stamens (> 50). Fruit rounded in cross section.	*C. ferruginea* L., *C. incana* HBK, *C. indica* (L.) Rawc. & Rendle.	New World
Sect. *Calanthea* DC.	Leaves large (more than 0.3 cm wide) and persistent. Flowers in simple or compound inflorescences (racemes, umbels, corymbs), although solitary flowers at the leaf axil may appear in some individuals. Sepals thin, linear, and pointed. Flowers with numerous stamens (> 50). Fruit rounded in cross section.	*C. nemorosa* Jacq., *C. pulcherrima* Jacq.	New World
Sect. *Capparidastrum* DC.	Stems generally thorny. Flowers in simple or compound inflorescences (racemes, umbels, corymbs), although solitary flowers at the leaf axil may appear in some individuals. Leaves large (more than 0.3 cm wide) and persistent. Sepals oval without gland. Flowers with numerous stamens (> 50). Gynophore short. Fruit rounded in cross section.	*C. brasiliana* DC., *C. macrophylla* HBK, *C. cuneata* DC.	New World
Sect. *Capparis*	Flowers always solitary at leaf axils. Plants with flowers slightly zygomorphic, abaxial sepal not galeate or slightly galeate. Flowers with numerous stamens (> 50).	*C. spinosa* L.	Old World
Sect. *Corymbosae* (DC.) Span. (= Subsect. *Corymbosae* DC., Sect. *Monostichocalyx* Radlk. p.p.)	Branches unarmed. Leaves large (more than 0.3 cm wide) and persistent. Flowers in corymbose inflorescences. Sepals rounded; gynophore very short or large. Flowers with numerous stamens (> 50). Fruit rounded in cross section.	*C. sepiaria* L., *C. umbellata* Brown ex DC., *C. incanescens* DC.	Old World
Sect. *Cynophalla* DC.	Stems generally thorny. Flowers in simple or compound inflorescences (racemes, umbels, corymbs), although solitary flowers at the leaf axil may appear in some individuals. Leaves large (more than 0.3 cm wide) and persistent. Sepals ovate possessing basal gland or foveole. Flowers with numerous stamens (> 50). Gynophore large. Fruit rounded in cross section.	*C. cynophallophora* L., *C. guayaquilensis* HBK, *C. amplissima* Lam.	New World

Table 1. Continued.

Infrageneric rank	Characters	Representative species	Distribution
Sect. *Galeatae* Inocencio et al.	Flowers always solitary at leaf axils. Plants with flowers strongly zygomorphic, abaxial sepal strongly galeate. Flowers with numerous stamens (> 50).	*C. cartilaginea* Decne.	Old World
Sect. *Quadrella* DC.	Leaves large (more than 0.3 cm wide) and persistent. Flowers in simple or compound inflorescences (racemes, umbels, corymbs), although solitary flowers at the leaf axil may appear in some individuals. Flowers with numerous stamens (> 50). Fruit angular in cross section.	*C. jamaicensis* Jacq., *C. intermedia* HBK, *C. crotonoides* HBK	New World
Sect. *Seriales* (DC.) Span. (= Subsect. *Seriales* DC., Sect. *Monostichocalyx* Radlk. p.p.)	Branches unarmed. Leaves large (more than 0.3 cm wide) and persistent. Inflorescences racemose or in series on the stems. Sepals rounded. Flowers with numerous stamens (> 50). Gynophore very short or large. Fruit rounded in cross section.	*C. zeylanica* L. *C. acuminata* Willd., *C. quadriflora* DC., *C. rotundifolia* Rottl., *C. brevispina* DC.	Old World
Sect. *Sodada* (Forssk.) Benth. & Hook.	Leaves thin, 0.3–2.0 × 0.1–0.3 cm, deciduous. Flowers in simple or compound inflorescences (racemes, umbels, corymbs), although solitary flowers at the leaf axil may appear in some individuals. Flowers with numerous stamens (8–18).	*C. decidua* (Forssk.) Edgew.	Old World
Subsect. *Octandrae* DC.	Branches unarmed. Leaves large (more than 0.3 cm wide) and persistent. Flowers in simple or compound inflorescences (racemes, umbels, corymbs), although solitary flowers at the leaf axil may appear in some individuals. Sepals rounded. Flowers with 8 stamens. Gynophore very short or large. Fruit rounded in cross section.	*C. racemulosa* DC., *C. oleoides* Burch., *C. coriacea* Burch.	Old World
Subsect. *Pedicellares* DC. (= Sect. *Monostichocalyx* Radlk. p.p., Sect. *Busbeckia* (Endl.) Benth. & Hook. p.p.)	Branches unarmed. Flowers geminate or in bunches of three, rarely alone. Leaves large (more than 0.3 cm wide) and persistent. Sepals rounded. Flowers with numerous stamens (> 50). Gynophore very short or large. Fruit rounded in cross section.	*C. horrida* L. f., *C. pubiflora* DC., *C. canescens* DC.	Old World

Table 2. List of morphological characters considered in the study.

Character	States
1. Plant habit	Erect / procumbent / pendulous
2. Height	Maximum length of the stems in meters
3. Twig shape	Tortuose / straight
4. Twig color	Green / yellowish / reddish / waxy
5. Internodes	Length in millimeters
6. Stipule shape	Curved / somewhat curved / straight / setaceous
7. Stipule orientation	Spreading / retrorse / antrorse
8. Stipule base	Decurrent / not decurrent
9. Stipule color	Orange-yellow / orange / golden-yellow
10. Leaf shape	Rounded / ovate / lanceolate / oblong / elliptical / obcordate /obovate
11. Base of the leaf	Obtuse/ tapering / acute/ cordate
12. Leaf apex	Acute / rounded / obcordate / obtuse / truncate
13. Mucro presence and length	Long (1–1.5 mm) / small (0.5–1 mm) / very small (0.1–0.5 mm) / lacking
14. Mucro shape	Straight / curved
15. Leaf texture	Herbaceous / fleshy
16. Leaf veins prominence	Prominent / not prominent
17. Petiole length	Very short (less than 0.5 cm) / short (0.5–1.5 cm) / long (exceeding 1.5 cm)
18. Leaf abaxial indument	Very dense / dense / dense to lax / lax / very lax
19. Trichome thickness	Thick (25–50 μm) / thin (15–25 μm)
20. Trichome length	Long (250–900 μm) / short (50–250 μm)
21. Fertile floral pedicel length	Long (greater than 4 cm) / short (1.5–4 cm)
22. Fertile floral pedicel thickness	Thick (over 1 mm) / slender (less than or equal to 1 mm)
23. Flower bud apex	Acute / rounded
24. Abaxial sepal	Galeate / slightly galeate
25. Flower symmetry	Zygomorphic / somewhat zygomorphic
26. Number of stamens	Numerous (100–150) / not so numerous (40–80)
27. Anther length	Very small (2 mm) / small (2–3 mm) / large (3 mm)
28. Anther apex	Rounded / acute
29. Fruit shape	Rounded / ellipsoidal / obovate / oblong
30. Pulp color	Red / yellow
31. Seed color	Brown/ dark brown
32. Seed size	Length × width × depth in millimeters

preparing exsiccatae. Voucher specimens were deposited in MUB and UMH.

Here we base species on morphological and biogeographical features. The species represented are more or less distinct, heterogeneous, and variable morpho-physiological entities, the origin of which is associated with a particular environment and area in agreement with Vavilov (1931). Taxa are defined in such a way that it is relatively easy to determine the ascription of each specimen to either one or another. Therefore, extremely large and variable species were avoided. Discontinuities, both geographical and morphological (see vestiture, stipules, leaves, inflorescences, flowers, and fruits sections in this paper), are good markers, but hybridization and hybrid swarms have obscured the definition of species and subspecies.

New taxa are represented in Figures 3, 6–9.

Geographic distributions have been plotted exclusively using the information from herbarium sheets. Distribution of species comprising several subspecies is represented in Figures 2, 4, and 5. Habitat is described using the available data on herbarium labels and those reported in the protologue of each taxa. Phenology data are restricted to the flowering-fruiting period according to the herbarium specimen labels and the protologue.

Taxonomic Characters in *Capparis* sect. *Capparis*

We have shown that molecular, phytochemical, and in vivo data are useful for understanding patterns of variation and, as such, were considered for the populations present in Spain, Morocco, Syria, and Lebanon (Inocencio, 2001; Inocencio et al., 2000, 2002, 2005); however, these methods have not yet been applied to the entire section. Therefore, we selected characters generally available in herbarium specimens (Table 2), some of which have been used for the first time in this study. For example, anther tip

Figure 1. Plant habit: —A. Erect, e.g., *Capparis zoharyi*. Drawn from photo taken in Llano del Beal, Murcia, Spain. —B. Procumbent, e.g., *C. spinosa*. Drawn from photo taken in Llubí, Mallorca, Spain. —C. Pendulous, e.g., *C. orientalis*. Drawn from photo taken in Palma de Mallorca, Spain.

shape was recognized as a useful character for identifying living, herbarium, and processed material (Inocencio et al., 2002); once characterized in fresh material, it is relatively easy to determine in herbarium specimens by re-hydrating the anthers and using a stereomicroscope. All the selected characters were studied in mature specimens with open flowers and ripe fruit. The quantitative characters are expressed using SI metric units.

PLANT HABIT IN *CAPPARIS* SECT. *CAPPARIS*

Capparis comprises small trees, shrubs, or geophytes. All species of section *Capparis* are erect, procumbent, or pendulous shrubs (Fig. 1). Some (*C. sicula*) behave as a true geophyte, with underground, branched perennial stems and decaying annual aerial parts (géothamne, sensu Bocquet & Aeschiman, 1981).

VESTITURE IN *CAPPARIS* SECT. *CAPPARIS*

Plants glabrous or with simple trichomes as the indument. Trichome types and the density of pubescence on various parts of the plant are useful characters for identifying some *Capparis* species. However, high infraspecific variation is common in collections identified as *C. sicula*, for example. More consistent vestiture is found on the abaxial part of the leaves, where density, thickness, and length of the indument (Table 1) may be analyzed for each taxon.

STIPULES AND LEAVES IN *CAPPARIS* SECT. *CAPPARIS*

Spiny stipules developing at the base of the petioles are absent in some species (e.g., *Capparis orientalis*) or are early shedding (e.g., *C. hereroensis*, *C. ovata*, *C. spinosa*). Stipule shape, color, direction of curvature and decurrence at the base are distinctive characters (Table 1).

Leaves are simple, not divided, alternate, with petioles well differentiated. Leaf morphology furnishes distinctive characters (shape, texture, base type, apex type, presence and type of mucro) (Table 2). The size and, much less, the shape of the leaves are variable within many species. Leaf size especially depends on water availability and exposure to winds and sun during the growing season. Petiole length, although variable within species, can be sorted into three groups (Table 2).

INFLORESCENCES AND FLOWERS IN *CAPPARIS* SECT. *CAPPARIS*

The flowers are solitary in the axil of the leaves. This is a distinctive character for the section. In other sections (except sect. *Galeatae*) the flowers form corymbose or racemose inflorescences. Flower buds may have acute or rounded apices. Flowers are bisexual and more or less zygomorphic. Four green sepals are always present, free, concave, having a more or less galeate (helmet-shaped) abaxial sepal. Four white or pink petals are always present, free, oval, frequently unequal. From 50 to numerous stamens. Anthers are small to large (Table 2) with a rounded or sharp apex; androphore absent. Nectary situated in the floral disk, between the insertion of the petals and sepals, triangular in form, apex directed toward the flower's interior. Nectary morphology can be a highly valuable taxonomic resource, but only available in fresh or well-preserved material (Inocencio et al., 2002). A gynophore is present, usually exceeding the stamens in length. The ovary is ellipsoid, situated at the end of the gynophore, unilocular, with (2 to)4(to 10) placentas.

FRUITS IN *CAPPARIS* SECT. *CAPPARIS*

The fruit is an oblong, ovoid, ellipsoid, or globose berry, that is green in color with well-defined longitudinal nerves, along which dehiscence later occurs. Seeds are from one to numerous, and are generally brown in color when mature, immersed in a reddish or yellow pulp. Seed shape, color, and dimensions have been noted to be of limited taxonomic value (Rivera et al., 2002).

TAXONOMIC TREATMENT

Capparis L., Sp. pl.: 503. 1753. TYPE: *Capparis spinosa* L.

Beautempsia Gaudich., Voyage Bonite Bot. Atlas: tab. 56. 1842 [1844–46]. TYPE: *Beautempsia avicenniaefolia* Gaudich., Voyage Bonite Bot. Atlas: tab. 56. 1842 [1844–46].

Busbeckea Endl., Prodr. Fl. Ins. Norf. 64. 1833. TYPE: *Busbeckea nobilis* Endl., Prodr. Fl. Ins. Norf. 64. 1833.

Colicodendron Mart., Flora 22(1) (Beibl.): 25. 1839. TYPE: *Colicodendron yco* Mart., Flora 22 (1) (Beibl.): 25. 1839.

Destrugesia Gaudich., Voyage Bonite Bot. Atlas: tab. 57. 1842 [1844–1846]. TYPE: *Destrugesia scabrida* Gaudich., Voyage Bonite Bot. Atlas: tab. 57. 1842 [1844–1846].

Hombak Adans., Fam. 2: 402, 408. 1763. TYPE: Genus described referring to Lippi MS. (Manuscript list of plants collected in Egypt by Lippi.) There are no species associated with the genus in the protologue. However, the inflorescence type, lack of leaves, and origin (Lippi, hence Egypt) likely refer to *Sodada decidua* Forssk. (= *Capparis aphylla* Roth).

Oligloron Raf., Sylva Telluriana: 109. 1838. TYPE: *Oligloron zeylanica* Raf.

Olofuton Raf., Sylva Telluriana: 108. 1838. TYPE: *Olofuton racemosum* Raf.

Pseudocroton Müll. Arg. Flora 55: 24. 1872. TYPE: *Pseudocroton tinctorius* Müll.
Quadrella (DC.) J. S. Presl, in Berchtold & J. S. Presl., Prirozenosti Rostlin 2: 260. 1825. TYPE: *Quadrella crotonoides* (Kunth) J. S. Presl. (= *Capparis crotonoides* Kunth. Nov. Gen. Sp. 5: 95. 1821).
Sodada Forssk., Fl. Aegypt.-Arab: 81. 1775. TYPE: *Sodada decidua* Forssk.
Uterveria Bertoloni, Pl. Nov. Hort. Bonon. 2: 8. 1839. TYPE: *Uterveria frondosa* Bertol.

Capparis section **Capparis** TYPE: *Capparis spinosa* L.

A total of 10 species and 12 subspecies of economic relevance are recognized, distributed in the tropical, subtropical, and Mediterranean zones of both hemispheres. Widely represented in Asia, and reaching southern Europe, eastern, northern, and southwestern Africa. A key for the species and recognized nothospecies of *Capparis* sect. *Capparis* is presented here.

KEY TO THE SPECIES OF *CAPPARIS* SECT. *CAPPARIS* IN ASIA, EUROPE, AND AFRICA

1a. Plants unarmed, or with stipules vestigial or caducous. Mediterranean Europe and North Africa [Albania, Algeria, Croatia, Greece, Italy, Libya, Malta, Spain, Turkey] . . . . 5. *C. orientalis*
1b. Plants always spiny 2
2a. Stipules retrorse to horizontally oriented 3
3a. Leaf texture somewhat fleshy 4
4a. Twigs yellow or gray-green, not glaucous, without waxy bloom; stipules golden yellow, not decurrent. Middle East [Afghanistan, Iran, Oman, Tajikistan, United Arab Emirates]. . . . . 1. *C. mucronifolia*
4b. Twigs green to red-purple, or glaucous due to a waxy covering; stipules orange, decurrent 5
5a. Shrubs erect; stipules strongly decurrent. Mediterranean Europe, North Africa, Middle East into Turkey [Algeria, Egypt, Greece, Israel, Jordan, Lebanon, Morocco, Spain, Syria, Turkey]. . . . . 10. *C. zoharyi*
5b. Shrub procumbent, or somewhat erect or pendulous; stipules decurrent to not decurrent 6
6a. Shrub pendulous; leaves lanceolate to ovate-lanceolate. North Africa [Algeria, Chad, Libya, Morocco, Tunisia] . . . . 6. *C. ovata*
6b. Shrub procumbent or somewhat erect; leaves rounded or obovate to ovate 7
7a. Shrub procumbent; twigs purple-red; without waxy bloom; leaves rounded, tip acute, base rounded to cordate. North Africa [Morocco] . . . . 2. *C. atlantica*
7b. Shrubs somewhat erect; twigs gray-green or glaucous, with waxy bloom; leaves obovate to ovate, bases and apices rounded. North Africa, Middle East into India [Egypt, India, Israel, Jordan, Saudi Arabia] . . . . 1. *C. aegyptia*
3b. Leaf texture herbaceous 8
8a. Flowers zygomorphic; abaxial sepal helmet-shaped, 1.7–2.5 cm long, 0.7–1.2 cm deep 9
9a. Shrub procumbent; stipules usually stout; pubescence on leaves from lax to very dense (rarely very lax). Mediterranean Europe, North Africa, Middle East into India [Afghanistan, Albania, Algeria, Azerbaijan, Cyprus, Georgia, Greece, India, Iran, Iraq, Israel, Italy, Jordan, Kazakhstan, Mongolia, Morocco, Pakistan, Saudi Arabia, Spain, Syria, Turkey, Turkmenistan, Ukraine, Uzbekistan, Yemen] . . . . 8. *C. sicula*
9b. Shrub procumbent or somewhat erect; stipules usually weak or vestigial, rarely stout; indument on leaves always very lax. Mediterranean Europe, Middle East into Turkey [France, Greece, Italy, Spain, Turkey] . . . . 9. *C. spinosa*
8b. Flowers slightly zygomorphic; abaxial sepal slightly galeate only to 1.4 cm long, to 0.6 cm deep. Middle East [Afghanistan, Iran, Iraq, Pakistan, Saudi Arabia, Turkmenistan] . . . . 7. *C. parviflora*
2b. Stipules mostly antrorse in orientation 10
10a. Shrub pendulous; mature leaves ovate; texture subcoriaceous; stipules curved. North Africa [Algeria, Chad, Libya, Morocco, Tunisia]. . . . . 6. *C. ovata*
10b. Shrub erect; mature leaves oblong to obovate; texture somewhat coriaceous; stipules setaceous. South Africa [Namibia] . . . . 3. *C. hereroensis*

1. Capparis aegyptia Lam., Encycl. Méthod. Bot. 1: 605. 1783. *Capparis spinosa* var. *aegyptia* (Lam.) Boiss., Fl. orient. 1: 420. 1867. TYPE: [Egypt] "Lipi á observé ce Caprier en Egypte (v.s. in herb Isn.)" (lectotype, designated here, P-JU!: specimen on sheet 11,248 right).

Capparis sinaica Veill., in Duhamel, Traité Arbr. Arbust. Ed. 2, Vol. I: 144. 1801. TYPE: [Egypt] "Habite. L'Arabie pétrée, sur le Mont Sinai et les montagnes qui l'environnent, auprès du village du Pharagou, et sur les chemins entre le Mont Sinai et le château ou la ville de Tor, situés sur la mer Rouge, oú il a été observé par Belón, Rauwolf et Shaw" (lectotype, t. 112 in Shaw, Cat. Pl. Variis Afr. 1738!, designated by Rivera et al. 2003a: 308–309).
Capparis deserti (Zohary) Täckh. & Boulos, Publ. Cairo Univer. Herb., 5: 14. 1972 [1974]. *Capparis spinosa* L. var. *deserti* Zohary, Bull. Res. Coun. Israel 8D: 56. 1960. TYPE: [Israel] Wadi Nosz, entrance to Wadi Lehiani (Bir Derheba), 27 Mar. 1944, *P. H. Davis & N. Feinbrun 5076–7* (holotype, HUJ!).

Shrub somewhat erect, glabrous; twigs straight, up to 3 m long, gray or blue green due to waxy cover that appears over the entire plant; internodes 1.5–4 cm; stipules curved, retrorse, slightly decurrent, orange, 0.3–0.4 cm long, 0.1–0.2 cm wide at the base. Leaves obovate to ovate, 2–3 × 1.8–3 cm, somewhat fleshy; leaf veins not prominent; bases and apices rounded; mucro very small, 0.1–0.5 mm, straight or curved; petioles 0.5–1 cm. Flower buds rounded; floral pedicels stout, 2.5–4 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate at apex, 1.4–1.6 cm long, 0.6–0.8 cm deep; stamens 30 to 80, anthers 1.2–1.5 mm, with rounded apices. Fruit

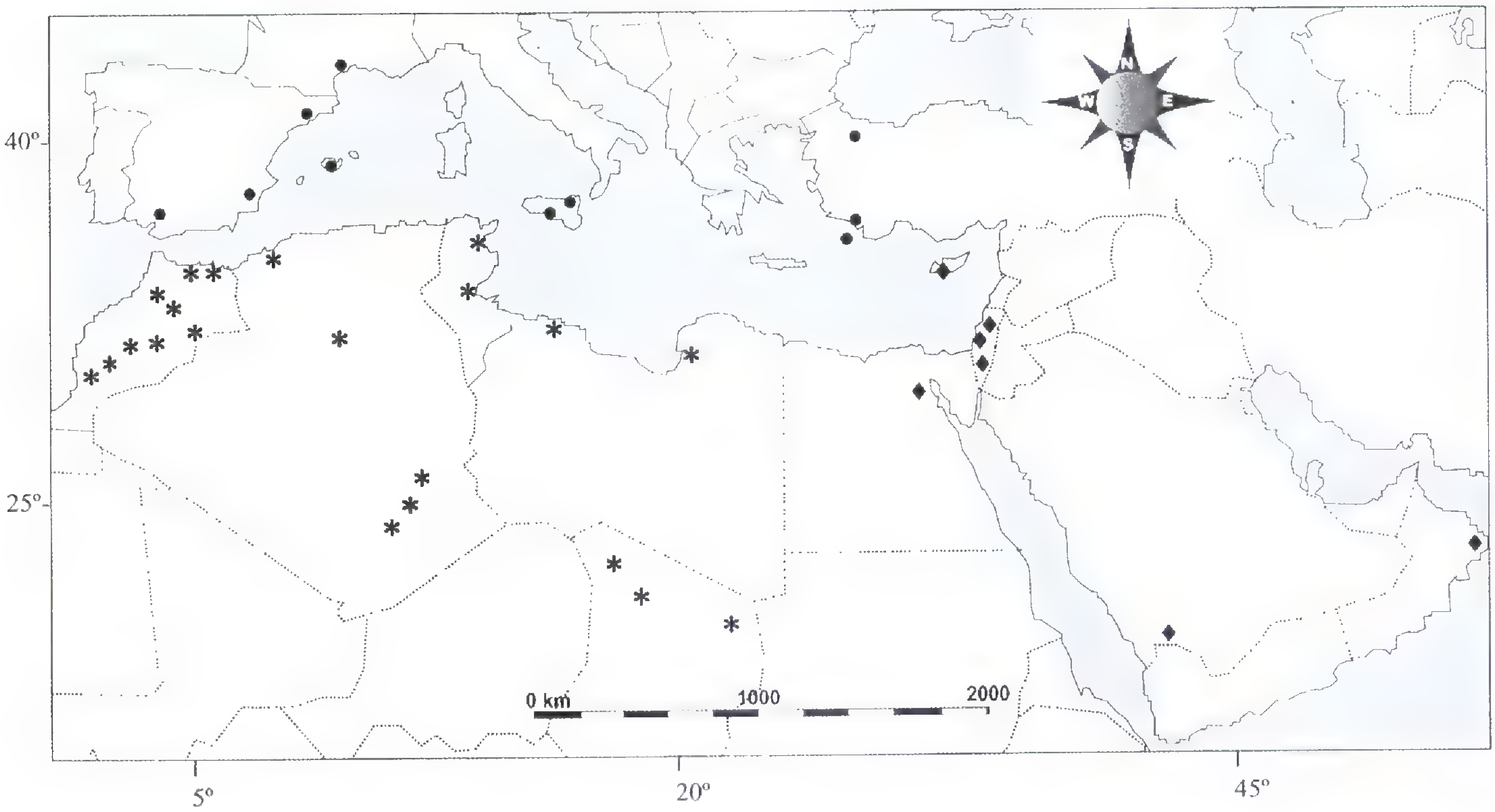

Figure 2. Distribution map for *Capparis ovata* (✻) (both subspecies); *Capparis spinosa* (●); and *Capparis aegyptia* (◆). *Capparis aegyptia* also occurs in India, beyond map range.

oblong, pulp color unknown; ripe seeds dark brown, 3.2–3.4 × 2.8–3 × 1.8–2 mm.

Illustrations. Plate 31(3) in Delile, 1812. Zohary (1960: 52, fig. 1). Täckholm. (1974: 163, pl. 48c). Migahid (1988: 48, pl. 26).

Phenology. Flowering and fruiting from (January) March to August (December).

Distribution and habitat. Saharo-Arabian, extending into the Irano-Turanian and Mediterranean Regions. North Africa, Middle East into India [Egypt, India, Israel, Jordan, Saudi Arabia]. Rocky places, steep slopes, at elevations from 0 to 2000 m, often in the vicinity of human dwellings. It is the common caper in Egypt and is often associated with the *Hyparrhenia hirta* (L.) Stapf community. Figure 2.

The type specimen of *Capparis aegyptia* has one flower, no fruits. It is part of the herbarium A. T. Danty d'Isnard, which is cited by Lamarck (1783): "v(idit) s(iccam) in herb(ario) Isn(ard)." It was included in 1857 in the Jussieu herbarium (P-JU). The specimen was collected "en face de Minia" in Egypt by one botanist who gave it to Isnard: "Doni per tu" [Gift for you]. It was, presumably, D. Lippi (1678–1704) himself. Isnard wrote the manuscript list of plants—now at P-JU—collected by Lippi in Egypt during his last trip in 1704 (Pritzel, 1872).

The basionym of *Capparis deserti* (Zohary) Täckh. & Boulos, *Capparis spinosa* L. var. *deserti* Zohary, was validly published by Zohary. However he states "This is a 'weak' variety because small-leaved forms occur almost in all groups."

Selected specimens examined. EGYPT. Cairo, *Schweinfurth 995* (K); Gebel Ez Zebir, Sinai, *Tadmor S-417* (K); Minia, *Lippi ?* (P); *Tadmor & Shmida S-420* (E); Sinai, *Bové 273* (K). INDIA. Mahablesham, Bombay, *T. C. s.n.* (E). ISRAEL. Nabulus, *Stait 266* (RNG); Wadi Qelt, *Davis 4888* (K); Ein Gedi, *Lyschede s.n.* (C); Kfar Gileh and Manara, *Curle 65* (K); Manara, *Curle 143* (E); Mount Gilboa, *Davis 1667* (E); Wadi Yarmuk, *Davis 4604* (E). JORDAN. Wadi Mujib, Ma'daba, *Boulos 5856* (K). SAUDI ARABIA. *Wadi Lakus, Jebel,* Collenette 7228 *(K).*

2. Capparis atlantica Inocencio, D. Rivera, Obón & Alcaraz, sp. nov. TYPE: [Morocco] "Safi, 20–6-1999. *Inocencio 60026*" (holotype, UMH!; isotypes, MO!, K!, E!, MA!). Figure 3.

Suffrutex decumbens, usque ad 60 cm, caulibus purpureis, foliis rotundis, apice acutis, base rotundatis, 1.5–3 cm longis, 1.2–2.5 cm latis, a *C. zoharyi* differt; stipulis tenuioribus, apicibus foliorum acutis nunquam rotundis nec cordatis a *C. zoharyi* et *C. aegyptia* differt.

Shrub procumbent, up to 60 cm high, glabrous; twigs straight, up to 2 m long, reddish purple, sometimes green; internodes 1–3 cm; stipules curved, retrorse, slightly decurrent, orange, 0.3–0.6 cm long, 0.2–0.3 cm wide at the base. Leaves rounded, 1.5–3 × 1.2–2.5 cm, somewhat fleshy; leaf veins not prominent; bases rounded to cordate, apices acute; mucro very small, 0.1–0.5 mm, straight; petioles short, 0.3–1 cm. Flower buds rounded; floral pedicels slender, short, 2–3 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 1.4–1.6 cm long, 0.5–0.6 cm deep; stamens 30 to 80, anthers very small, 1.8–2 mm, apices rounded. Fruit oblong, pulp

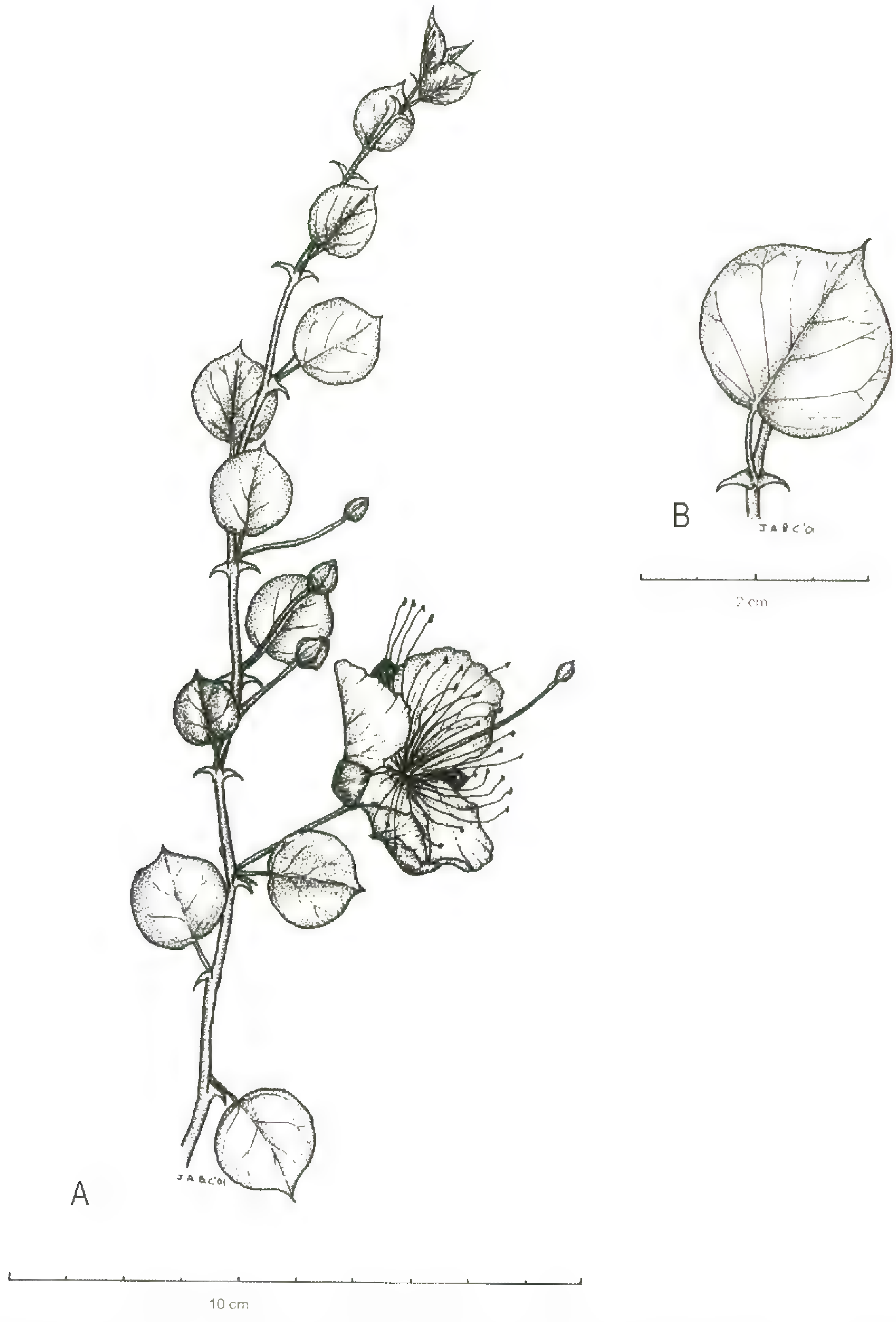

Figure 3. Details of the new species *Capparis atlantica* Inocencio, D. Rivera, Obón & F. Alcaraz. —A. Stem and flower. —B. Detail of leaf. (A, B drawn by J.-A. Barreña from *Inocencio 70100*, UMH.)

color unknown; ripe seeds brown, 2.4–2.6 × 2.2–2.4 × 1.6–1.8 mm.

Phenology. Flowering and fruiting from May to August.

Distribution and habitat. Mediterranean Region. North Africa [Morocco]. It is the common caper species in the High Atlas Mountains of Morocco. Found in rocky places, slopes, on calcareous substrata or marls, occasional on metamorphic substrata; at elevations from 0 to 2000 m, often in the vicinity of human dwellings. In the surroundings of Moulay Brahim (Morocco), it grows on clayey slopes along with *Ephedra* L. sp., *Teucrium fruticans* L., *Lavandula* L. sp., *Chamaerops humilis* (*J. C. Archibald, 4586*, E). Figure 4.

Capparis atlantica is a procumbent shrub with purple-red twigs; *C. aegyptia* is somewhat erect with gray-green or glaucous twigs; and *C. zoharyi* is erect. The stipules are not so strongly decurrent in *C.*

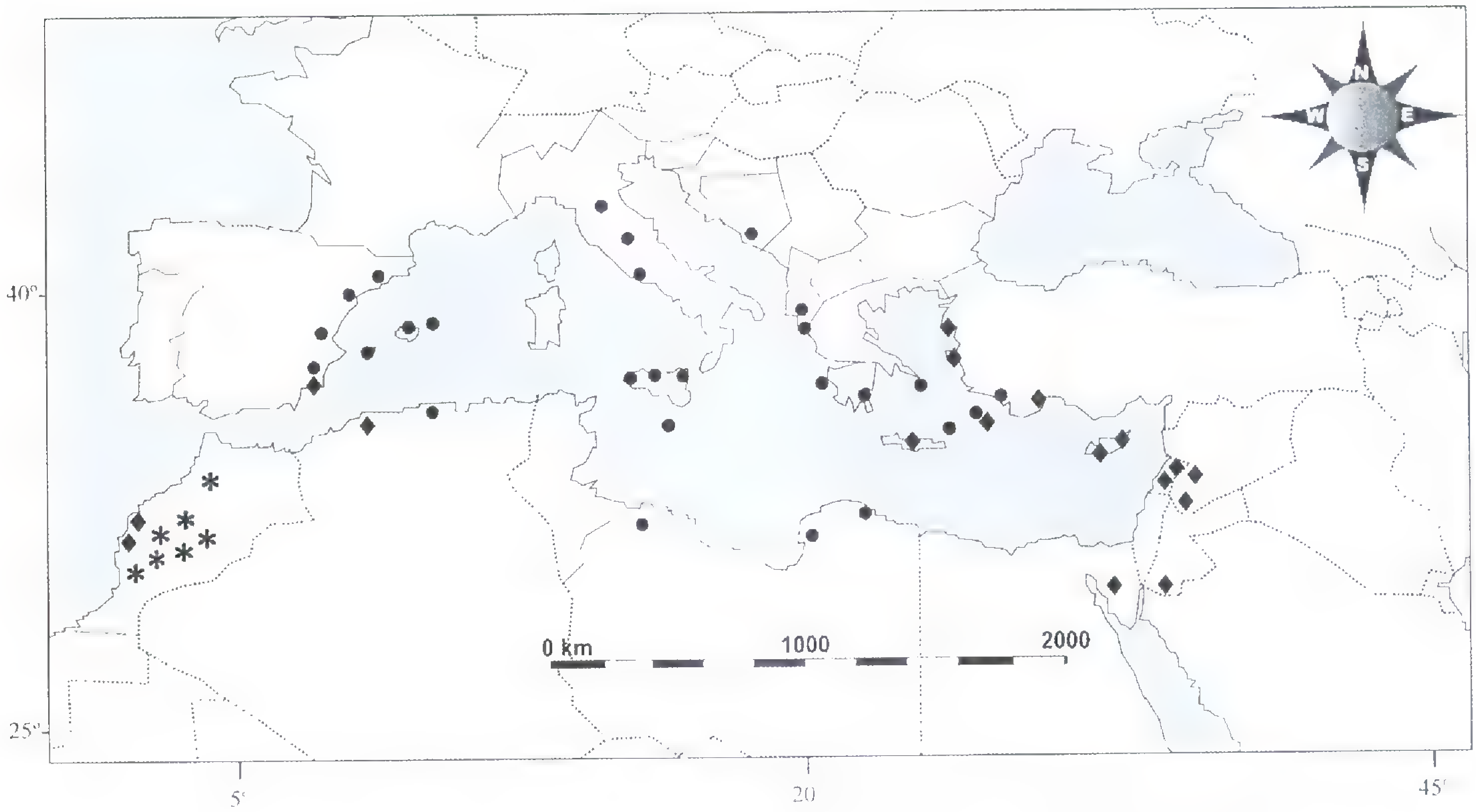

Figure 4. Distribution map for *Capparis atlantica* (✻); *Capparis orientalis* (●); and *Capparis zoharyi* (◆).

atlantica as in *C. zoharyi*; the leaf tips of *C. atlantica* are acute, while those of *C. aegyptia* and *C. zoharyi* are rounded.

Paratypes. MOROCCO. Asni, *Inocencio 60005* (UMH); falls of Ouzoud, *Jury 8764* (RNG); Marrakech, *Jury 8783* (RNG); Moulay Brahim, *Archibald 4586* (E); Oued Argaoui, *Inocencio 60003* (UMH); Siksoua, Greater Atlas, *Hooker s.n.* (K); Tafraoute, *s.n. 468* (RNG); Tizi n'test, *Inocencio 60034* (UMH).

3. **Capparis hereroensis** Schinz, Bull. Herb. Boissier 1(3): 396. 1895. TYPE: [Southwest Africa = Namibia] "Südwestafrika: Zwischen Wortel und Walfischbai, October 1886, *Schinz 1006*" (lectotype, designated here, Z!).

Shrub erect, almost glabrous; twigs straight, up to 3 m long, yellowish green; internodes 1.3–2.5 cm; stipules antrorse, mostly setaceous, not decurrent, sometimes falling or weak, yellow, 0.2–0.3 cm long, 0.05–0.1 cm wide at the base. Leaves oblong-obovate, 2.3–4.2 × 1–1.6 cm, somewhat fleshy, yellowish green; leaf veins prominent; bases tapering to rounded, apices rounded to somewhat truncate; mucro small, 0.5–1.0 mm, straight; petioles 0.5–1 cm. Flower buds rounded; floral pedicels thick and short, 2.5–4.5 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 1.6–1.8 cm long, 0.6–0.8 cm deep; stamens 30 to 80, anthers 2.5–3 mm, with acute apices. Fruit ellipsoidal, pulp color unknown; ripe seeds dark brown, 3.8–4 × 3.6–3.8 × 2.7–3 mm.

Phenology. Flowering from January to April.

Distribution and habitat. Karoo-Namib Region. South Africa [Namibia]. Dune-forming sandy substrate, in coastal zones; at elevations from 0 to 100 m.

The Schinz herbarium is at Z. At Z there are two sheets with type material of *Capparis hereroensis* because holotype is not designated in the protologue. The specimen accompanied by a single handwriting on the sheet with the following text, "*Capparis hereroensis* Schinz/Wortel, Walfischbai/1886/2 Bogen/N° 1006," is here designated as the lectotype; the specimen on the other sheet, with identical Schinz collection number, is a paralectotype.

Selected specimens examined. NAMIBIA. Walvis Bay Town, Salworks, *Ward 9250* (K); Hereroland, Walfischbai, *Schinz 1006* (Z); Conception Hut, *Ward & Ward 158* (K).

4. **Capparis mucronifolia** Boiss., Diagn. Pl. Orient., Ser. 1, Vol. 1: 3. 1843. *Capparis spinosa* L. var. *mucronifolia* (Boiss.) Hedge & Lamond, Fl. Ir. Hoch. Umr. Geb.: 7. 1970. TYPE: [Iran or Oman] "Hab. in Persia Australi et Regno Mascatensi, *Aucher 4189*. . ." (lectotype, designated here, G!).

Key to the Subspecies of *Capparis mucronifolia* in the Middle East and Central Asia

1a. Twigs slightly tortuose; stipules curved, retrorse; leaves ovate, pubescence very lax; flower buds acute at apex . . . . a. *C. mucronifolia* subsp. *mucronifolia*

1b. Twigs straight; stipules almost straight or somewhat curved, retrorse or often spreading; leaves

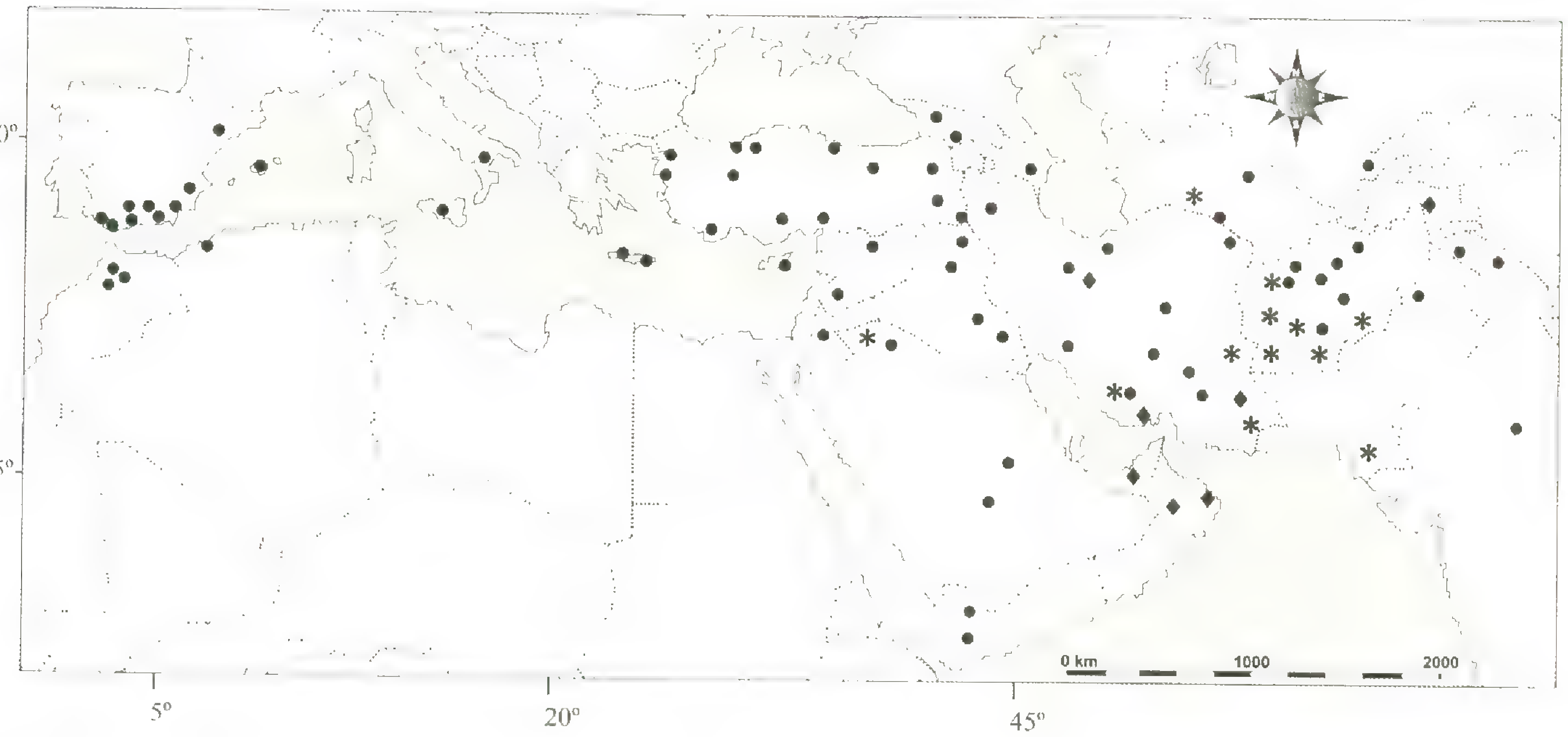

Figure 5. Distribution map for *Capparis parviflora* (✱) (three subspecies); *Capparis sicula* (●) (all five subspecies); and *Capparis mucronifolia* (◆) (both subspecies).

oblong-lanceolate, pubescence lax; flower buds rounded . . . . . b. *C. mucronifolia* subsp. *rosanoriana*

Distribution. Figure 5.

4a. Capparis mucronifolia Boiss. subsp. **mucronifolia**

Capparis elliptica Hausskn. & Bornm. ex Bornm. var. *maskatensis* Hausskn. & Bornm. ex Bornm., Mitt. Thür. Bot. Ver. N.F. VI: 49. 1894. TYPE: [Oman] "foliis latioribus ovatis; in rupibus ad Maskat, [*J. Bornmüller*] *ex. 46*" (lectotype, designated here, JE!).

Shrub somewhat erect, heavily branched, irregularly and widely spreading, up to 1 m high; twigs slightly tortuose, approximately 2 m long, yellowish or grayish green; internodes 0.5–3 cm; stipules curved, retrorse, not decurrent, golden yellow, apex orange, sometimes pubescent, at least basally, 0.2–0.6 cm long, 0.1–0.2 cm wide at the base. Leaves ovate, 2–4 × 0.5–1.5 cm, somewhat fleshy; indument very lax, trichomes thick and short to long, (20)30–40 × 200–400 µm; leaf veins not prominent; bases usually rounded, sometimes tapering, apices acute; mucro small, 0.5–1.0 mm, straight; petioles very short, 0.2–0.4 cm. Flower buds acute; floral pedicels slender, short, 2.5–3.5 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 1.4–1.6 cm long, 0.7–0.9 cm deep; stamens 30 to 80, anthers 1.3–1.5 mm, with round apices. Fruit oblong, pulp color unknown; ripe seeds brown, 2.4–2.8 × 1.6–2 × 1.6–1.8 mm.

Phenology. Flowering from March to September.

Distribution and habitat. Sudano-Zambezian and Saharo-Arabian, extending to the Irano-Turanian Regions. Middle East [Afghanistan, Iran, Oman, United Arab Emirates]. Rocky slopes, ravines and stony plains of deserts, wadies in *Acacia seyal* Del. hammada, at elevations from 0 to 1000 m.

There is no designation of holotype for *Capparis mucronifolia* by Boissier; the type material cited comprises different specimens collected by P. M. R. Aucher Eloy in southern Iran and Oman (former kingdom of Muscat), with collection numbers 4189, 4190, and 4192, during his travels in 1835–1838. Therefore lectotypification is needed. The sheet with the lectotype contains the following labels: I "*Capparis mucronifolia* / Boissier". II "Aucher-Eloy-Herbier d'Orient N . 4189." Paratypes are Aucher pl. exs. 4190 and 4192, G!. Isolectoypes are in K!

Capparis elliptica Hausskn. & Bornm. ex Bornm. Mitt. Thür. Bot. Ver. N.F. VI: 49. 1894, is a later homonym of *Capparis elliptica* Span. ex F. Muell. Fragmenta Phytographiae Australiae 9: 172. 1875; it is within the range of *Capparis mucronifolia* subsp. *mucronifolia*.

There is no designation of holotype for *Capparis elliptica* var *maskatensis* Hausskn. & Bornm.; the type material cited comprises different specimens collected, under number 46, by J. Bornmüller in his "Iter Persico–turcicum 1892–1893." Haussknecht's herbarium is at JE; Bornmüller worked from 1904 as curator in JE, but sold his herbarium to B. Most of the Bornmüller Capparidaceae material at B was destroyed during the Second World War. One *Capparis* specimen with collection number 46 is at JE (J. Müller, pers. comm.). Therefore lectotypification is needed and possible. The sheet with the lectotype contains the following labels: I "Isotypus/ *Capparis elliptica* Hausskn. & Bornm./ var. *maskatensis* Hausskn. & Bornm." II "J. Bornmüller: Iter Persico-

turcicum/ 1982–93/ No 46/ *Capparis spinosa* L. v./ *Maskatensis* Hsk. & Bornm./ determ.:/ Arabia australis: in saxosis ad Maskat/ 1893. 25–5 legit: J. Bornmüller."

Selected specimens examined. AFGHANISTAN. Griffith, *Lemann 374* (K). IRAN. Bangar Langeh, *Davis & Bokhari, D. 56176* (E); Chahbahar, Baluchistan, *Runemar 22417* (E); Zahedan, *Gray-Wilson & Hewer 263* (K); Hormuz, *J. Bornmüller 5* (K). OMAN. Istal, Wadi Bani Kharus, *Radcliffe-Smith 4045* (K); Ruwi near Muscat, *Miller 6003* (E). UNITED ARAB EMIRATES. Hatta, Dubai, *Western 267* (E); Fujairah, *Lumley 38* (K).

4b. Capparis mucronifolia Boiss. subsp. **rosanoviana** (B. Fedtsch.) Inocencio, D. Rivera, Obón & Alcaraz, comb. et stat. nov. Basionym: *Capparis rosanoviana* B. Fedtsch., Beih. Bot. Centralbl. 20: 297. 1906. *Capparis rosanoviana* B. Fedtsch., Consp. Fl. Turk. Vol. II: 98. 1909. TYPE: [Tajikistan] "Ost-Buchara: am östlichen Abhange der Berge Aryktau, höher als Goranty, auf Felsen, 1900–2000', am 3. [= 15.] April 1883 (*A. Regel!*)." (lectotype, designated here, LE!).

Shrub somewhat erect, well branched from base, irregularly and widely spreading, up to 1 m high; twigs straight, erect or decumbent, up to 2 m long, yellowish or grayish green; internodes 1–2 cm; stipules almost straight or somewhat curved, retrorse, often spreading, not decurrent, yellow-golden, 0.2–0.4 cm long, 0.1–0.2 cm wide at the base. Leaves oblong-lanceolate, 1.5–2 × 0.4–2 cm, somewhat fleshy; indument very lax, trichomes thick and long, 20–30 × 200–400 μm; leaf veins not prominent; base usually rounded, apices acute; mucro long, 1–1.5 mm, straight; petioles very short, 0.1–0.3 cm. Flower buds rounded; usually with indument at least at the base; floral pedicels slender, short, 2–3 cm; flower shape unknown. Fruit unknown; ripe seeds unknown.

Illustrations. Bobrov (1939: 7, tab. 1, fig. 2; 1970: 8, tab. 1, fig. 2).

Phenology. Flowering and fruiting from July to August (Bobrov 1939: 3; 1970: 5).

Distribution and habitat. Irano-Turanian Region. Middle East [Tajikistan]. At the eastern slope of the mountains Aryktau, above Goranty and on the left bank of the River Vakhsh, between Kurgan-Tyube and Lechman. Limestone, sunny rocky slopes, and sandy substrata; from 600 to 1500 m. Also in the Kafimigan, Pani, and Amudarya river valleys, in southwestern Tajikistan (Anonymous, 2005).

According to Regel (in sched., LE), the fresh flowers display a corolla with yellowish tints, and the staminal filaments are reddish. The dried fruits are oblong-lanceolate, with marked longitudinal nerves (Fedtschenko & Fedtschenko, 1906).

There is no designation of holotype by B. Fedtschenko; the type materials cited are different specimens collected by E. A. von Regel in southwestern Tajikistan (former Bukhara region) during his travels in 1883. Therefore lectotypification is needed. Two sheets have been found by Vladimir Dorofeev in LE containing type material. The sheet with the lectotype contains the following label: I "A. Regel, Iter Turkestanicum/ In decliv. Orient. montium Aryktau [am östlichen Abhange der Berge Aryktau]/ supra Horanty [höher als Goranty] 1200–2000'/ 3–15/ VIII 1883." The sheet with the paralectotype contains the labels: I "August 1883/ 14/ Sandstrecken zwischen Kurgantüfe/ und Lechman, 1200–1300'/ (links Wachschufer)." II "A. Regel, Iter Turkestanicum/ Sandstrecken zwischen Kur-/ gantüfe und Lechman 1200–1300'/ (links Wachschufer)" (LE!).

Selected specimens examined. TAJIKISTAN. Kadajian, *s.n. 277* (E); between Kurgan Tyube and Lechman, *Regel s.n.* (LE); eastern slopes of Aryktau mountain, *Regel s.n.* (LE).

5. Capparis orientalis Veill., in Duhamel, Traité Arbr. Arbust. ed. 2, 1: 142. 1801. *Capparis spinosa* L. subsp. *orientalis* (Veill.) Jafri, Flora of Libya, Vol. XII: 3. 1977. TYPE: "*Capparis non spinosa fructu majore* C. Bauh. Pin. 480. . ." (lectotype, designated by Rivera et al. (2006), the image in J. Bauhin, J. Cherler & D. Chabrey, Hist. Plant. Vol. II: 63. 1651!; epitype, designated by Rivera et al. (2006), [Greece] Sokastro, Dodecanese, *Th. Raus 8382*, E!).

Capparis rupestris Sm., Fl. Graec. Prodr. Vol. I: 355. 1809. *Capparis spinosa* L. subsp. *rupestris* (Sm.) Nyman, Consp. Fl. Eur.: 68. 1878. *C. spinosa* L. var. *rupestris* (Sm.) Hook. f. & Thoms., in Hook. f., Fl. Brit. India Vol. I: 173. 1872. TYPE: [Greece, Crete] "In Cretâ et Antiparo insulis, ad rupes" (lectotype, designated here, OXF!).

Shrub pendulous or decumbent, sometimes reaching great dimensions in shaded sites, glabrous; twigs straight, dark green, sometimes reaching more than 3 m long; internodes 2–7 cm; plants unarmed, occasionally vestigial stipules are early falling. Leaves rounded, or somewhat ovate, 3–8.5 × 2.3–8 cm, somewhat fleshy; leaf veins not prominent; base rounded, sometimes cordate, apices obtuse, sometimes obcordate, rarely acute; mucro lacking or very small, 0.1–0.5 mm; petioles long, 1–2.5 cm. Flower buds rounded, rarely acute; floral pedicels thick and long, 5–8 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 1–1.5 cm long, 0.6–

0.8 cm deep; stamens 30 to 80, anthers 2–3 mm, with round apices. Fruit ellipsoidal, with apices nipple-shaped, pulp red; ripe seeds dark brown, 3.2–3.6 × 2.8–3 × 2.8–3 mm.

Illustrations. Figure 1 in Ali & Jafri (1977: 5). Guerau & Torres (1981: 31).

Phenology. Flowering from May to October.

Distribution and habitat. Mediterranean Region. Mediterranean Europe and North Africa [Albania, Algeria, Croatia, Greece, Italy, Libya, Malta, Spain, Turkey]. Rocks, cliffs, walls of old buildings, at elevations from 0 to 600 m, often surrounding human dwellings. Figure 1.

Capparis orientalis was described by Veillard in Duhamel (1801: 142), apparently fundamentally based on the pre-Linnaean literature. He gives three synonyms, listing the authors and references where these have appeared previously. Also, further material is cited in pages 142–143, after the discussion of the species. The references to the habitat and distribution are restricted to: "Les rochers de l'isle de Crète et des isles de l'Archipel, particulièrement celle d'Antiparos; en Syrie et dans la Palestine." Both localities and bibliographical references—including illustrations—furnish fundamental elements for determining the original material of Veillard. The author himself places different values on the material used. Part of the material is only indirectly cited in the discussion after the protologue, in which several additional authors, localities, and icon are cited. The new species is not illustrated in the original paper. Veillard's herbarium is unknown because it was apparently part of the missing Duhamel herbarium (Stafleu & Cowan, 1976). Thus the only original materials available for typification are the two images cited by Veillard. The remaining references are unillustrated. Lonicer's icon (Lonicer, 1679: 106) may be discarded, as Veillard himself noted the poor quality of this drawing. However, it clearly represents an unarmed caper bush with rounded leaves. The illustration in Bauhin et al. (1651: 63) is cited by Veillard in the pre-Linnaean synonymy of *C. orientalis* and was selected as lectotype by Rivera et al. (2006).

According to Veillard in Duhamel (1801), this species was collected in Palestine and Syria by travelers such as Pockocke and Shaw. We have not found any plant material of this species from the Levant, neither from these collectors nor others. However, it is likely that the species occurred in the area.

There is no designation of holotype for *Capparis rupestris* Sm. Serena Marner (pers. comm.) did find a single specimen (one blossoming branch and a branch with a young fruit) of *Capparis rupestris* in one sheet of the Sibthorpian Herbarium at OXF corresponding to the Fl. Graec. Prodr. Vol. I: 355. 1809, number 1190, which is also associated with Fl. Graec. T. 487. The sheet of *Capparis rupestris* is a very typical one from the Sibthorpian Herbarium. The cited illustration [Tab. 487] was later published (Smith, 1825); however, it is also original material. The citation "Folia quam in praecedente crassiora et succo pleniora. Olivier" is certainly Olivier (1801–1807). Guillaume Antoine Olivier was a French naturalist who traveled in Greece, Turkey, the Levant, and other Middle Eastern countries between 1792 and 1798. Therefore, lectotypification is needed. We have seen the sheet (OXF) with the lectotype, which contains neither references to localities nor collectors. However it is clearly labelled "C. rupestris/Sib." [written in the hand of J. E. Smith] and "J. Sibthorp, M.D." [None of the material has the localities written directly on the sheets in the Sibthorpian Herbarium at OXF.] The specimen is typical of a specimen collected on the first voyage in 1786 or 1787 (Serena Marner, pers. comm.). It is in agreement with the description in the protologue. The sheet contains further stamp and annotation with reference to the Prodromus Flora Graeca [added by M. A. Lawson, Sherardian Professor of Botany at Oxford (Lack, 1997)]. Therefore, the specimen is reasonably original material and is designated here as a lectotype.

Selected specimens examined. ALBANIA. Berirk Saranda, *Krendl s.n.* (C); Sarandë, *Alston 2248* (K). ALGERIA. Cape Carbon, Bejaia, *Davis 52961* (E). CROATIA. Cavtat, *Larsen s.n.* (C); Lapad, Dubrovnik, *Larsen s.n.* (C); Dubrovnik, *Clement s.n.* (RNG). GREECE. Argolis, Tolon, *Bowen 6507* (RNG); Karpathos, Islet Sokastro, *Davis 8382* (E); Sokastro, Dodecanese, *Th. Raus 8382* (E); Kiklades, Andros, *Jury 271* (RNG); Corfu, Markos, *Davis 54537* (E); Gerolimenas, *28379* (C); Island Zakynthos, *Boratynski 728* (C); Port Kheli, *Lewis 642* (K); Rhodes, *Ahaussen s.n.* (C). ITALY. Florence, *s.n.* (C); Palermo, *R. Coll 314* (E); Perugia, *Ransone 410* (E); Pisa, *Savi 429* (K); Rome, *Larsen 4874* (C); Sicily, Taormina, Island Bella, *Ostenfeld s.n.* (C); Messina, *S. P. Brookes 5754* (RNG); Favignana, Cape Calarossa, *J. R. Akeroyd 545* (RNG); Island Leranzo, *Davis 40174* (RNG). LIBYA. Coefia, N of Benghazi, *Davis 50477* (E); Gebel Nefoussa, *Davis 49670* (E); Kouf, *J. H. H. L 26* (K); Shahat, *Ali 624* (E). MALTA. Addaloute Cemetery, *Lanfranco 5967* (RNG); Malta, *Wright s.n.* (K). SPAIN. **Alicante:** *Gram 2039* (C); Santa Barbara Castle, *Inocencio & Alcaraz 60048* (MUB). **Barcelona:** Barcelona, *Sennen 1587* (RNG). **Ibiza:** Santa Eulalia, *Cannon 3256* (RNG). **Mallorca:** Palma de Mallorca, *Inocencio & Alcaraz 48696* (MUB); Alcudia, *Inocencio & Alcaraz 18697* (MUB); Valldemosa, *Jacobsen s.n.* (C). **Menorca:** Punta Nati, *Rita s.n.* (RNG). **Tarragona:** Benifavet, *Inocencio & Alcaraz 18701* (MUB). **Valencia:** Lliria, *Inocencio & Alcaraz 18700* (MUB). TURKEY. Mugla Province, Marmaris District, *Prance 116* (E).

6. Capparis ovata Desf., Fl. Atlant., Vol. I: 404. 1798. *Capparis spinosa* L. var. *ovata* (Desf.) Batt., in Batt. & Trabut., Fl. Algérie: 82. 1888. TYPE: [Algeria] "Habitat in fissuris rupium prope Oran" *s.c.* (lectotype, designated here, P 948!).

KEY TO THE SUBSPECIES OF *CAPPARIS OVATA* IN THE MEDITERRANEAN REGION, THE MIDDLE EAST AND NORTH AFRICA

1a. Young leaves usually ovate to ovate-lanceolate, mature leaves ovate, 2.5–5 × 2–4.5 cm; stipules antrorse . . . . a. *C. ovata* subsp. *ovata*
1b. Young leaves usually lanceolate, mature leaves ovate-lanceolate, 2.5–4 × 0.9–1.9 cm; stipules retrorse . . . . b. *C. ovata* subsp. *myrtifolia*

Distribution. Figure 2.

6a. Capparis ovata Desf. subsp. **ovata**

Capparis sicula Veill. var. *kruegeriana* Pamp., L'Agricoltura Col. 22: 459. 1926. *Capparis spinosa* L. var. *rupestris* forma *kruegeriana* (Pamp.) Pamp., Prodr. Fl. Ciren.: 234. 1931. *Capparis spinosa* L. subsp. *orientalis* (Veill.) Jafri. var. *kruegeriana* (Pamp.) Jafri., Flora of Libya. Vol XII: 4. 1977.

Shrub pendulous, sometimes reaching great dimensions in shaded sites; twigs straight, up to 3 m long, dark green or with a reddish tint in younger twigs, adult ones becoming woody, acquiring grayish or brown color; internodes 1.5–2.5 cm; stipules curved, mostly antrorse, sometimes spreading, not decurrent, sometimes very small or early falling, yellow, 0.15–0.4 cm long, up to 0.1 cm wide at the base. Leaves usually ovate, when young ovate to ovate-lanceolate, 2.5–5.5 × 2–4.5 cm, subcoriaceous; indument lax, trichomes thick and short, 30–40 × 200–250 μm; leaf veins not prominent; base usually rounded or somewhat tapering, apices acute; mucro small, 0.5–1 mm, straight; petioles short, 0.5–1 cm. Flower buds acute; floral pedicels thick, long, 4.5–6.5 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 1.5–1.7 cm long, 0.7–0.9 cm deep; stamens 30 to 80, anthers 2–3 mm, with round apices. Fruit obovate, pulp yellow; ripe seeds dark brown, 2–2.2 × 2.2–2.4 × 1.6–1.8 mm.

Illustrations. P. Ozenda (1991: 246, fig. 68); Lewalle & Montfort. (1997: 25); A. Benchelah et al. (2000: 147); Charco (2001: 283).

Phenology. Flowering from April to December.

Distribution and habitat. Saharo-Arabian and Mediterranean Regions. North Africa [Algeria, Libya, Morocco, Tunisia]. On rocks or walls of old buildings, at elevations from 0 to 2000 m, often in the vicinity of human dwellings.

Selected specimens examined. ALGERIA. Ahaggar, Tezzeit, 1750 m, *Maire 180* (P); Bejaia, *Reverchon s.n.* (E); Djanet, Tamli of Tafalelet, *Lhote 107* (P); Oranais, *Faure s.n.* (E). LIBYA. Coefia, Benghazi, *Davis 50477* (RNG); Gebel Nefoussa, Giado, *Davis 49678* (RNG); Tripolitania, Tarhunah, *Keith 1038* (K). MOROCCO. Driouch, *Inocencio 60029* (MUB); Gorge du Ziz, Er-Rachidia, *Jury 17819* (RNG); Fez, *Mateos 6653/95* (RNG); Imzoûrene, *Jury 15602* (RNG); Msemrir, Dadés, *Jury 17776* (RNG); Nador, Kebdana, *Romo 6501* (RNG); Ouarzazate, *Brooks E.5349* (RNG); Dj. Sarhoro, Ouarzazate, *Davis 53476* (E); River Yanoile, *Inocencio 60021* (MUB); Safi, *Inocencio 60024* (MUB); Taroudannt, *Jury 14453* (RNG); Taza, *Jury 8602* (RNG); Sidi Belkassen, *Ratherford s.n.* (RNG); Tnant, *Ratherford BV1281/93* (RNG); Tazeka, *Jury 16777* (RNG); Zaio, *Inocencio 60000* (MUB). TUNISIA. Kabylia, *Letourneux s.n.* (P); Khargued, *Letourneux s.n.* (P); Fedj el Kheirs, *Letourneux s.n.* (P).

The sheet 948 at P contains two branches with leaves and without flowers or fruits; the specimen to the right is selected as a lectotype. It is labelled as "Herbier de la Flore Atlantique/ doné au Muséum par Desfontaines/ N°/ Capparis ovata." Another label states "Habitat in fissuris rupium prope Oran." In the protologue, Desfontaines also cites seven pre-Linnaean references associated with images of a *Capparis* species known since at least the 1st century AD from the coasts of Marmarica (northern Libya and Egypt), which is without doubt *Capparis ovata* s. str. However, other authors interpreted these as belonging to *C. spinosa* or *C. sicula*.

Candolle (1824) raised the question of homonymy with *Capparis ovata* M. Bieb. On account of this supposed homonym he proposed naming the species from Algeria with the type material by Desfontaines: *Capparis fontanesii* DC. Prodr. Vol. I : 245. 1824. TYPE: "in fissuris rupium Mauritaniae prope Oran. . . v.s. sine fl. in h. Desf." There is no reason to adopt this view of Candolle because *C. ovata* M. Bieb. is a later homonym (Bieberstein, 1808).

6b. Capparis ovata Desf. subsp. **myrtifolia** Inocencio, D. Rivera, Obón & Alcaraz, subsp. nov. TYPE: [Chad] "Habitat in fissuris rupium Enneri Gousa, Tibesti, 3000', 15 Mar. 1953, *Guichard KG/TIB/40*" (holotype, the specimen with the label "KG/TIB/40", P!).

Foliis angustis lanceolatis, stipulis valde retrorsis a typo differt.

Shrub pendulous, sometimes reaching great dimensions in shaded sites; twigs straight, dark green or with a reddish tint in younger twigs, adult ones becoming woody, acquiring grayish or brown color; internodes 1.5–2.5 cm; stipules curved, retrorse, not decurrent, 0.2–0.4 cm long, up to 0.1 cm wide at the base. Leaves usually ovate-lanceolate, the young leaves usually lanceolate, 2.5–4 × 0.9–1.9 cm, subcoriaceous; indument lax, trichomes thick and short, 30–40 × 200–250 μm; leaf veins prominent; base somewhat tapering, apices acute; mucro small, 0.5–1 mm,

straight; petioles short, 0.5–1 cm. Flower buds acute; floral pedicels thick and long, 4.5–6.5 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 1.2–1.5 cm long, 0.5–0.7 cm deep; stamens 30 to 80, anthers 2–3 mm, with round apices. Fruit obovate, pulp yellow; ripe seeds dark brown, 2–2.2 × 2.2–2.1 × 1.6–1.8 mm.

Phenology. Flowering from (September)January to March.

Distribution and habitat. Saharo–Arabian Region. North Africa [Algeria, Chad]. On rock crevices, from 1000 to 2000 m.

The *Capparis ovata* populations of the Central Sahara mountains show distinct retrorse stipules (as most species in section *Capparis*) in contrast to *C. ovata* populations of North Algeria and Morocco which have mostly antrorse, sometimes spreading, not decurrent, sometimes very small or early-falling stipules. The type of stipules is a character very distinct and constant. The leaves are narrower and the floral pedicels are longer in the Central Sahara specimens. This led us to distinguish this new subspecies, that is subordinated to *C. ovata*. Otherwise it has some likeness to *C. cartilaginea* Decne., which is also present in the area, but the strongly zygomorphic flowers of the latter species (which we included in another section) are not found in *C. ovata* subsp. *myrtifolia*.

Paratypes. ALGERIA. Darmouilly, W of Tamanrasset, *Chipp 28* (K); Tamanrasset, *Chipp 28* (P). CHAD. Aouzi, Tibesti, *Dalloni s.n.* (P); Ennerdi, Tibesti, *Dalloni s.n.* (P); Gozou, Ennerdi, *St. Serole 57* (P); Gorges L'Oudingueur, Tibesti, *Brookt 52* (K); Enneri Gousa, Tibesti, 1000 m, *Guichard s.n.* (P).

7. Capparis parviflora Boiss., Diagn. Pl. Orient., Ser. 1, Vol. I: 4. 1843. *Capparis spinosa* var. *parviflora* (Boiss.) Boiss., Fl. Orient. Vol. I: 420. 1867. *Capparis leucophylla* DC. var. *parviflora* (Boiss.) Zohary, Bull. Res. Council Israel 8 D: 59. 1960. TYPE: [Iran] "Hab. in Persia australi. *Aucher pl. exs. N 4191 et 4191 A*" (lectotype, designated here, G!, G8503).

KEY TO THE SUBSPECIES OF *CAPPARIS PARVIFLORA* IN THE MIDDLE EAST AND CENTRAL ASIA

1a. Fruit oblong or elliptical; twigs yellow green; mature leaves ovate-rounded, 0.5–2.5 × 0.5–2 cm, pubescence from dense to almost glabrous . . 2

2a. Fruit oblong; mature leaves ovate-rounded, 0.5–2 × 0.5–2 cm; pubescence from dense to lax . . . . a. *C. parviflora* subsp. *parviflora*

2b. Fruit ellipsoidal; mature leaves ovate-lanceolate, rarely obovate, 1–2.5 × 0.7–2 cm; pubescence almost glabrous . . . . . b. *C. parviflora* subsp. *kurdica*

1b. Fruit rounded; twigs yellow green to gray-white; mature leaves obovate to ovate-rounded, 0.7–1 × 0.6–1 cm; pubescence dense . . . . c. *C. parviflora* subsp. *sphaerocarpa*

Distribution. Figure 5. This *Capparis* species shows a geographical pattern of variation.

7a. Capparis parviflora Boiss. subsp. **parviflora**

Capparis murrayana Graham, Cat. Pl. Bombay: 9. 1839. TYPE: [India] "On veins of trap rock in the bottom of ravines at Mahableshwur [Mahabaleshwar], rare; at Loghur (*Sir C. Macolm.*) - about Hurrychunderjee (*Dr. Gibson*)" (not seen).

Shrub procumbent, up to 75 cm high; twigs straight, up to 2 m long, light green or yellowish green; internodes 0.5–1.5 cm; stipules somewhat curved, retrorse, not decurrent, golden yellow, contrasting with the twigs, 0.3–0.5 cm long, 0.1–0.2 cm wide at the base. Leaves ovate-rounded, 0.5–2 × 0.5–2 cm, herbaceous; indument variable from dense to lax, trichomes thin and long, 20–25 × 300–900 μm; leaf veins not prominent; base acute to tapering, apices rounded or acute; mucro very small, 0.1–0.5 mm, straight; petioles very short, 0.3–0.5 cm. Flower buds rounded or slightly acute; floral pedicels slender, short, 1.5–2.5 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 1.2–1.4 cm long, 0.5–0.6 cm deep; stamens 30 to 80, anthers 1.3–1.5 mm, with round apices. Fruit oblong, pulp red; ripe seeds brown, 2–2.2 × 1.8–2 × 1.6–1.9 mm.

Phenology. Flowering and fruiting from (April)May to September.

Distribution and habitat. Irano-Turanian and Saharo-Arabian Regions, extending to the Sudano-Zambezian Region. Middle East and Central Asia [Afghanistan, Iran, Pakistan, Saudi Arabia, Turkmenistan]. Cliffs, stony places, and slopes, in semi-deserts; from 650 to 1850 m.

A holotype was not designated for *Capparis murrayana* Graham (1839). The John Graham Herbarium has not been found.

Selected specimens examined. AFGHANISTAN. Herat, *Hedge & Lamond s.n.* (K); Kandahar Pirzada, *Edelberg 2052a* (C); Kandahar Pirzada, *Hedge & Lamond 2052a* (C); Kajakay, *Petersen 152* (E); Kajakay, *Hedge & Lamond 2142* (C); Province of Chakhansur, 2 km to the N of Lashe Jowayn, *Breckle 4928* (E); Shin Dand, 10 mi. S, *Furse s.n.* (K); Zint Gorge, Mam district, 8 June 1958, *Chapman 26096* (K). IRAN. Fars, Kuh-i-Bamus, Schiras, *Archibald 2940* (E); Kuh-e-Hari, *A. J. Lee 83* (K); Schiras, *Kotschy 309* (E); Schiras, *Hohenacker 309* (C). PAKISTAN. Tando Jan, *Jafri 2406* (E). SAUDI ARABIA. Aflja Well, *J. D. Dwyer 13125* (RNG); Turayf, *Collenette 4495* (K). TURKMENISTAN. Ashjabat, *s.n.* (E).

7b. Capparis parviflora Boiss. subsp. **kurdica** (Zohary) Inocencio, D. Rivera, Obón & Alcaraz, stat. et comb. nov. Basionym: *Capparis ovata* Desf. var. *kurdica* Zohary, Bull. Res. Council Israel, Vol. 8D, 56. 1960. TYPE: [Iraq] "Rupes Mt. Singarae [Djabal Sindjar], Mai 1867 *C. Haussknecht s.n.*" (holotype, K!).

Shrub procumbent, almost glabrous; twigs straight, up to 2 m long, yellowish green; internodes 1.5–3 cm; stipules somewhat curved, retrorse, somewhat to very widely spreading, not decurrent, golden yellow, contrasting with the light twigs, 0.2–0.4 cm long, 0.1–0.2 cm wide at the base. Leaves ovate-lanceolate, rarely obovate, 1–2.5 × 0.7–2 cm, herbaceous; leaf veins not prominent; base rounded or somewhat tapering, apices acute to rounded; mucro very small, 0.1–0.5 mm, straight; petioles very short, 0.3–0.5 cm. Flower buds rounded; floral pedicels slender, short, 2–3.5 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 0.9–1.2 cm long, 0.4–0.6 cm deep; stamens 30 to 80, anthers 1.5–1.8 mm, with rounded apices. Fruit ellipsoidal, pulp red; ripe seeds dark brown, 3.2–3.8 × 2.2–2.6 × 2.4–2.2 mm.

Phenology. Flowering from June to September.

Distribution and habitat. Irano Turanian Region. Middle East [Afghanistan, Iran, Iraq]. Cliffs, ravines, in stony places, from 200 to 700 m.

Selected specimens examined. AFGHANISTAN. Chakhansur, Zaranj, *Breckle 4905* (E). IRAN. Avroman, Schahu, *Haussknecht s.n.* (K). IRAQ. Bilas, *Raui 29409* (K); Darvidikhan, *1536* (E); Zint gorge, Mam district, *Chapman 26096* (K).

7c. Capparis parviflora Boiss. subsp. **sphaerocarpa** Inocencio, D. Rivera, Obón & Alcaraz, subsp. nov. TYPE: [Afghanistan] "Herat:105 Km S Herat versus Shindand, *K. H. Rechinger, Iter Orientale 1967/37579*" (holotype, E!). Figure 6.

Foliis minoribus, usque ad 1 cm longis latisque, fructibus brevioribus globosis non oblongis a typo differt.

Shrub procumbent, up to 75 cm high; twigs straight, up to 2 m long, yellowish green or grayish-whitish; young twigs very thin with very short internodes (0.1–0.3 cm) and very spiny; longer adult twig internodes 0.3–1 cm; stipules somewhat curved, retrorse, usually very open, slightly spreading to widely spreading, slightly decurrent to not decurrent, golden yellow contrasting with whitish twigs, 0.3–0.5 cm long, 0.1–0.2 cm wide at the base. Leaves obovate to ovate-rounded, the young rounded, 0.7–1 × 0.6–1 cm, herbaceous; indument dense, trichomes thin and long, 20–25 × 350–800 μm; leaf veins not prominent; bases tapering to rounded, apices rounded or weakly acute; mucro very small, 0.1–0.5 mm, straight; petioles very short, 0.1–0.3 cm. Flower buds rounded; floral pedicels slender, short, 1.5–2 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 0.8–1.1 cm long, 0.3–0.6 cm deep; stamens 30 to 80, anthers 1.2–1.5 mm, with round apices. Fruit rounded, pulp red; ripe seeds dark brown, 2.6–2.8 × 1.6–1.8 × 2.3–2.8 mm.

Phenology. Flowering and fruiting from (April) May to August(September).

Distribution and habitat. Irano-Turanian Region. Central Asia [Afghanistan, Turkmenistan]. Cliffs and stony slopes, from 600 to 2000 m.

The sheet with the holotype (at E) is labelled as follows: I "K.H. Rechinger, Iter Orientale 1967/ 37579/ *Capparis spinosa* L./Var. *parviflora* (Boiss.) Boiss./Sw-Afghanistan, Herat:/105 Km S Herat Versus Shindand, 1300 M." II "Det. Hedge & Lamond, 1968/ 7.VIII."

Paratypes. AFGHANISTAN. Chakhansur, Zaranj, *Breckle 4928* (E); Fariah, *Hedge, Wendelbo & Ekberg W 7674* (E); Herat, *Hedge & Lamond 37579* (K); Shind Dand, *Furse 5488* (K). TURKMENISTAN. Asjabad, *Vikitin & Ivanov s.n.* (E).

8. Capparis sicula Veill., in Duhamel, Traité Arb. Arbust., Ed. 2, 1: 159. 1801. *Capparis ovata* var. *sicula* (Veill.) Zohary, Bull. Res. Council of Israel. 8D: 55. 1960. *Capparis spinosa* subsp. *sicula* (Veill.) Holmboe, Borg. Mus. Skr. Ny Raekke. Bird I, 2: 1–344. 1914. TYPE: [Italy] "Capparis Sicula duplicata spina, folio acuto. Boccone, 1666 [1674]. Icon. et descript. Rarior. Plantar. Sicil. P. 79. tab. 42. f. 3. Cupani Hort. Cathol. P. 36" (lectotype, designated by Rivera et al., 2006, Boccone's image, Icones et descriptiones rariorum plantarum Siciliae, Melitae, Juliae et Italicae: 79. tab. 42. f. 3. 1674!).

Key to the Subspecies of *Capparis sicula* in the Mediterranean Region, North Africa, the Middle East, and Central Asia

1a. Plants with stipules straight, spreading . . . . 8b. *C. sicula* subsp. *herbacea*
1b. Plants with stipules curved, retrorse 2
2a. Leaf pubescence lax, very lax, or almost glabrous . 3
3a. Twigs dark green; leaf pubescence lax, trichomes thick and long, 20–50 × 400–800 μm; floral pedicel thick and long, 5.5–7 cm . . . . 8a. *C. sicula* subsp. *sicula*
3b. Twigs light green, white, or yellow; leaves glabrous or with very lax pubescence, trichomes thin and short, 15–20 × 100–250 μm; floral pedicel slender and short, 1–4.5 cm 4
4a. Leaf pubescence very lax; stipules curved, retrorse, yellow-orange; anthers small, 2–2.5 mm. . . . . 8d. *C. sicula* subsp. *mesopotamica*

1b. Leaf almost glabrous; stipules somewhat curved, retrorse or spreading, golden yellow contrasting with the light color of twigs; anthers very small, 1.6–2 mm . . . . 8e. *C. sicula* subsp. *sindiana*
2b. Leaves appearing white due to dense pubescence . . . . 8c. *C. sicula* subsp. *leucophylla*

Distribution. Figure 5.

8a. Capparis sicula subsp. **sicula**

Capparis spinosa var. *canescens* Coss., Anal. Sci. Nat., 11: 28. 1849. *Capparis spinosa* subsp. *canescens* (Coss.) A. & O. Bolòs, Misc. Fontsere: 88. 1961. *Capparis ovata* Desf. var. *canescens* (Coss.) Heywood, Feddes Repert. 69: 56. 1964. TYPE: [Spain] "In rupestribus oppiduli Buenavista prope Xerez (*E. Bourgeau, pl. Esp. 1849, n. 43*)" (lectotype, designated here, P!).
Capparis ovata var. *palaestina* Zohary, Bull. Res. Council Israel 8D: 55. 1960. TYPE: [Israel] Upper Galilee, Wadi Hindaj, 25 June 1954, *M. Zohary 110* (holotype, HUJ!).

Shrub procumbent; twigs straight, sometimes reaching up to 3 m long, dark green; internodes 1.5–5 cm; stipules curved, retrorse, not decurrent, occasionally slightly decurrent, yellow-orange, 0.3–0.6 cm long, 0.2–0.3 cm wide at the base. Leaves ovate, oblong or elliptic, 3–5 × 2–4.5 cm, herbaceous; indument lax, trichomes thick and long, 20–50 × 400–800 μm; leaf veins not prominent; base rounded or somewhat tapering, apices acute; mucro long, 1–1.5 mm, usually curved; petioles short, 1–1.5 cm. Flower buds acute; floral pedicels thick and long, 5.5–7 cm; flowers zygomorphic; abaxial (odd) sepal galeate, 1.7–2.5 cm long, 0.7–1.2 cm deep; stamens 100 to 150, anthers 2.5–3 mm, with acute apices. Fruit oblong, pulp red; ripe seeds dark brown, 2.6–3 × 2.4–2.8 × 2–2.2 mm.

Illustrations. Boccone (1674: 79, tab. 42, f. 3); Zohary (1966: 359); Valdés et al. (1987: 374); Castroviejo et al. (1993: 520, pl. 142); Plitmann et al. (1983: 81); O. Fragman et al. (2001: 312–3, pl. 133).

Phenology. Flowering May to October.

Distribution and habitat. Mediterranean and Irano-Turanian Regions; locally introduced in the Saharo-Arabian Region. Mediterranean Europe, North Africa, Middle East into Turkey [Albania, Algeria, Cyprus, Greece, Italy, Morocco, Spain, Syria, Turkey]. Stony places, marls or clayish soils, scrubs, at elevations from 0 to 600 m; in the vicinity of human dwellings.

Selected specimens examined. ALBANIA. Below Levani and Frascula district, M. Barat, *Baldaci 197* (K). ALGERIA. Orán, *Faure s.n.* (K). CYPRUS. Cape Greco, *Gold 29* (RNG). GREECE. Baths of Eretria, Island Euboea, *Stamatiadhou 17290* (C); Crete, Kissamos, *Bickerich 15091* (K); Irakliou, *Bowen 8913* (RNG); Fokis, Delfi, *Pinset 107* (RNG); Island Poros, *Strid 29680* (C); Mitilini, Lesbos, *Hansen 4918* (C); Valimiú, Peloponessos, *Hanson 67-1-1* (RNG). ITALY. Basilicata, Potenza, *Akeroyd 3328* (RNG); Gigerti, Agrigento, *Tavalione s.n.* (C). MOROCCO. Fez, *Inocencio 60016* (MUB); Khénichèt, *Inocencio 60014* (MUB); Meknès, *Jury 15502* (RNG); Sidi-Kareen, *Inocencio 60017* (MUB). SPAIN. **Alicante:** Reservoir of Amadoiro, *Alcaraz 48705* (MUB); La Algueña, Crevillente, *Inocencio & Alcaraz 48683* (MUB). **Almería:** Santa María de Nieva, *David 1017* (RNG); Níjar, *Inocencio & Alcaraz 48712* (MUB); Berja, *Inocencio & Alcaraz 48710* (MUB); Cañada de Vélez, Orce, *Inocencio & Alcaraz 48714* (MUB); Las Cuadras de D. Pepe, Velez Rubio, *Inocencio & Alcaraz 48682* (MUB); Los Lobos, *Inocencio & Alcaraz 48723* (MUB); Church of Saliente, Chirivel, *Inocencio & Alcaraz 48713* (MUB); Huércal-Overa, *Inocencio & Alcaraz 48728* (MUB); Serón, *Inocencio & Alcaraz 48678* (MUB); Sierra de Gador, *Valdés 813* (RNG). **Cádiz:** Jerez, *Inocencio & Alcaraz s.n.* (MUB); Sanlúcar, *S. Silvestre 2524/68* (RNG). **Granada:** Castillejar, *P. F. Cannon 692* (RNG); Malá, *Gardner 1337* (RNG); Lanjarón, *Inocencio & Alcaraz 48718* (MUB); Reservoir of Negratín, *Inocencio & Alcaraz 48703* (MUB); Guadix, *Inocencio & Alcaraz 48712* (MUB); Loja, *Inocencio & Alcaraz 48681* (MUB); Baza, *Inocencio & Alcaraz 48680* (MUB); Salobreña, *Inocencio & Alcaraz 48717* (MUB). **Huesca:** Velilla de Cinca, *Inocencio & Alcaraz 48688* (MUB). **Málaga:** Torre del Mar, *Inocencio & Alcaraz 48688* (MUB); Velez Málaga, *Inocencio & Alcaraz 48719* (MUB). **Mallorca:** from Palma de Mallorca to Andraitx, *Inocencio & Alcaraz 48726* (MUB). **Murcia:** Santa Cruz del Calvario, *Lange s.n.* (C); Murcia, *Lange s.n.* (C); Venta del Olivo, *Inocencio & Alcaraz 48708* (MUB); Barinas, *Inocencio & Alcaraz 48704* (MUB); Albudeite, *Inocencio & Alcaraz 48709* (MUB); Lorca, *Inocencio & Alcaraz 48722* (MUB); Yéchar, *Inocencio & Alcaraz 48711* (MUB). **Jaén:** Alcaudete, *Inocencio & Alcaraz 48721* (MUB); from Larva to Guadiana Menor, *Inocencio & Alcaraz 48727* (MUB); Jódar, *Inocencio & Alcaraz 48720* (MUB). **Sevilla:** Osuna, *Inocencio & Alcaraz 48679* (MUB); S of Spain, *J. W. Carr 20706.6* (RNG). SYRIA. Djebel Casioun, Damascus, *Sammuelsson 1518* (K). TURKEY. Ankara, *Davis & Coode 37217* (E); Dardanelles, *s.n.* (E); Denizli, *K. Hormia 588* (RNG); Erzurum, Oltu, *Baytop 14366* (E); Hakkari, Zab river, *Trelawny 1305* (E); Keslitürkmenli, Mersin, *Hennipman 1073* (RNG); Pamukkale, Denizli, *Baytop 10231* (E); Saraycik-Osmancik, *Tobey 2569* (E).

8b. Capparis sicula subsp. **herbacea** (Willd.) Inocencio, D. Rivera, Obón & Alcaraz, stat. et comb. nov. Basionym: *Capparis herbacea* Willd., Enum. Pl.: 560. 1809. *Capparis ovata* var. *herbacea* (Willd.) Zohary, Bull. Res. Council Israel 8D: 56. 1960. TYPE: [Russia, Georgia or Azerbaijan] "Capparis herbacea. Marschall a Bieberstein. Habitat ad Caucasum" (lectotype, designated here, B!, unlabelled blossoming specimen, B-W, folder 10034, right of sheet 2).

Capparis herbacea Willd. var. *microphylla* Ledeb., Fl. Ross.: 235. 1842. *Capparis leucophylla* DC. var. *microphylla* (Lebed.) Täckh. Students' Flora of Egypt, Ed. 2: 164. 1974. TYPE: [Kazakhstan or Turkmenistan] "Hab. ad litt. Orient.m. Caspii! *Karelin*" (holotype, LE not seen).

Shrub procumbent; twigs straight, sometimes reaching up to 3 m long, light green, herbaceous; internodes 1–3 cm; stipules straight, spreading, not

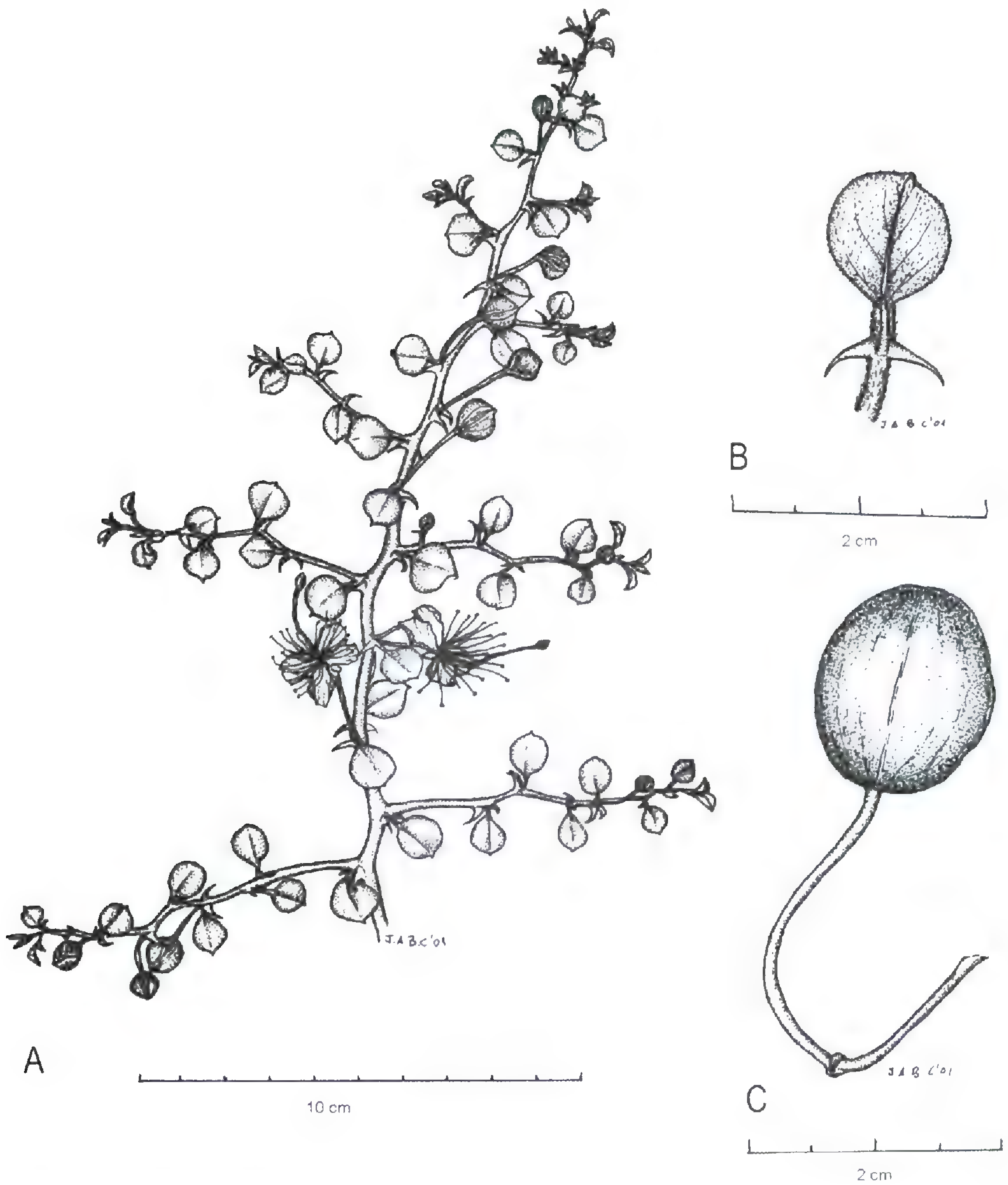

Figure 6. Details of the new subspecies *Capparis parviflora* subsp. *sphaerocarpa* Inocencio, D. Rivera, Obón, & Alcaraz. —A. Stems and flowers (drawn by J.-A. Barreña from *Furse 5488*, K). —B. Detail of leaf and stipules (drawn by J.-A. Barreña from *Nikitin & Ivanov s.n.*, E). —C. Fruit (drawn by J.-A. Barreña from *Hedge & Lamond 37579*, E).

decurrent, golden yellow, 0.3–0.6 cm long, 0.1–0.2 cm wide at the base. Leaves elliptic or oblong, 3–6 × 1.5–4 cm, herbaceous; indument lax, trichomes thin and short to long, 15–20 × 200–500 μm; leaf veins prominent; bases rounded, apices obtuse to acute; mucro small, 0.5–1 mm, curved; petioles short, 1–1.5 cm. Flower buds acute or rounded; floral pedicels thick and long, 4–6 cm; flowers zygomorphic; abaxial (odd) sepal helmet-shaped, 1.8–2.4 cm long, 0.6–1.2 cm deep; stamens 100 to 150, anthers 2.3–3 mm, with acute apices. Fruit obovate to oblong, pulp red; ripe seeds dark brown, 3–3.6 × 2.4–2.8 × 2–2.4 mm.

Note. Mongolian populations display stouter stipules and smaller leaves.

Illustrations. Takhtajan. (1966: 58, tab. 22).

Phenology. Flowering from May to September.

Distribution and habitat. Irano-Turanian Region extending to the Euro-Siberian. Middle East, Central Asia, and Caucasus [Afghanistan, Azerbaijan, Georgia, Iran, Kazakhstan, Mongolia, Turkey, Turkmenistan, Ukraine, Uzbekistan]. Stony places in calcareous soils and rocky grounds, slopes of low hills and walls of abandoned buildings, at elevations from 0 to 2000 m.

Selected specimens examined. AFGHANISTAN. Bamian, Darrah Siakar, *Hedge 3423* (E); Den Hundie, *Edelberg* 1889 (C); Kundut, Khanabad, *Carter 390* (K); Obeh, Herat, *Hedge W7777* (E); Samangan, *Hewer 1128* (E); Takhar, Mughul, *Podlech 11377* (E); Yawarzan, Badkshan, *Hedge W9471* (E). AZERBAIJAN. Morghak, from Parsabad to Bileh Savar, *Lamond 3097* (E). GEORGIA. S.l., *Frierk s.n.* (E); Caucasus, *Hohenanker s.n.* (E); Tbilisi, *Campbell 175* (K). IRAN. Amol, *Andersen 244* (E); Khvoy, *Cowan 1560* (K); Mazandaran, Elburz, *Furse & Synge 491* (K); Mianeh, *Bowles 2423* (K); Moraweh Tappeh, *Hewer H3804* (E); Sanganeh, Kopet Dagh,

Ghorashi-Al-Hosseni 495G (RGN). KAZAKHSTAN. Tchavto-gorozi loshnee sel. Tamerlanovski, *Priajin s.n.* (K). MONGOLIA. Tian-Shan, Mongolia, *Potanin s.n.* (K); Eastern Mongolia, Gobi, *Prezwalski s.n.* (K). TURKEY. Artvin, Coruh, *Davis & Hedge D32427* (E); Hakkari, Kalolans, *Davis 23870* (E); Kagizman, *Watson 375* (K); Karabük, *Baytop 11383/65902* (E); Kars, *Davis 46680* (E) (K); Konya, Akyokus, *Dural 576* (E); Osmaniye, *Balls 1199* (K); Sinop, Kargi, *Tobey 2809* (E); Tokat-Niksar, *Davis 24882* (K); Zonguldak, Karabuk, *Davis & Coode D39050* (E). TURKMENISTAN. Aschabad, *Freyn 260b* (E); Syr-Darja, *Golike s.n.* (K). UKRAINE. Krym, Yalta, *Toige 1896* (RNG). UZBEKISTAN. Altyn Tepe, Tashkent, 490 m, *Vasak s.n.* (K); Chauvast, Samarkand, *Paulsen 277* (C).

There is a clear reference in the protologue to the Caucasus, which indirectly points to the specimens from this area in the herbarium Willdenow (surprisingly the protologue does not mention the Mussin-Pushkin expedition, vid. infra.). The reference in the protologue to a "Capparis herbacea. Marschall a Bieberstein" is presumably pointing to *Capparis ovata* M. Bieb (Bieberstein, 1808, 1819). In the herbarium Willdenow (B) are two sheets within folder nr. 10034 pertaining to *Capparis herbacea* (Hiepko, 1972). The folder is labelled: "Polyandria Monogynia/ Capparis herbacea foliiis/ subrotunde ellipticis ovalis/ axillis spinosis. Pedunculis/ unifloris/ Habitat Caucasus." Sheets 1 and 2 are numbered and annotated both as follows: "C. herbacea" and "W." The folder has two other labels: "Mussin Pushkin/ W." This refers to Count Apollo Apollosovich Mussin-Pushkin (1760–1805), who was a Russian explorer and plant collector. He led a botanical expedition to the Caucasus in 1800–1802. The other label is almost illegible. It is not clear whether the specimen was originally collected in the Caucasus by Mussin-Pushkin or, presumably, cultivated in the Royal Botanic Garden of Berlin from seeds gathered by this collector (the species is published in a catalog of plants actually grown at Berlin). This species was, in fact, cultivated in another botanic garden in Saint Petersburg: "Cultam in tepidario saepe fruticosam fieri et C. spinosae assimilari nunciat Fischer in litteris" [Friedrich Ernst Ludwig von Fischer was director of the Imperial Botanic Garden of Saint Petersburg (Pritzel, 1872)] (Bieberstein, 1819).

8c. Capparis sicula Veill. subsp. **leucophylla** (DC.) Inocencio, D. Rivera, Obón & Alcaraz, stat. et comb. nov. Basionym: *Capparis leucophylla* DC., Prodr. Vol. I: 246. 1824. TYPE: [Iraq] "Inter. Bagdad et Alep. *Oliv. et Brug.* (v.s. in Herb. Mus Par.)" (lectotype, designated here, P!).

Capparis spinosa L. var. *pubescens* Zohary, Bull. Res. Council Israel 8D: 56. 1960. TYPE: [Egypt] Galala, rocks, 4100 ft., 1944, *P. H. Davis 8062* (holotype, K!).

Shrub procumbent; twigs straight, semi-erect, sometimes reaching up to 3 m long, glaucous; internodes 1.5–5 cm; stipules curved, retrorse, not decurrent or somewhat decurrent, golden yellow, 0.3–0.6 cm long, 0.1–0.3 cm wide at the base. Leaves elliptic to rounded, sometimes ovate, 2.5–4.5 × 2–3.5 cm, herbaceous; indument very dense, whitish, trichomes thin and long, 20–25 × 200–500 µm; leaf veins not prominent; bases rounded, apices obtuse or acute; mucro long, 1–1.5 mm, straight or somewhat curved; petioles short, 0.5–1 cm. Flower buds rounded or acute; floral pedicels thick and short, 2.5–3.5 cm; flowers zygomorphic; abaxial (odd) sepal galeate, 1.5–2.2 cm long, 0.7–1.1 cm deep; stamens 100 to 150, anthers 3.5–4 mm, with acute apices. Fruit oblong, pulp red; ripe seeds dark brown, 2.7–3 × 2.6–2.8 × 1.8–2 mm.

Illustrations. Mandaville (1990: pl. 69–70).

Phenology. Flowering from May to September.

Distribution and habitat. Irano-Turanian and Saharo-Arabian Regions. North Africa, Middle East into Pakistan [Afghanistan, Iran, Iraq, Israel, Pakistan, Saudi Arabia, Yemen]; also in Egypt (Zohary, 1960). Oasis in semi-deserts, flooding plains, sometimes in somewhat saline soils; at elevations from 0 to 1000 m.

The sheet with the lectotype of *Capparis leucophylla* is labelled: I "Capparis leucophylla DC/ (De Candole Script.)" II "de Bagad à Alep./ Olivier de Bruguiere" III "Herb. Mus. Paris./ Capparis leucophylla DC." The coincidence between labels and references to type material in the protologue led us to suppose Candolle was implicitly designating a holotype, provided the author used only one element.

Selected specimens examined. AFGHANISTAN. Baghlan, SW of Doshi, *Hewer 1153* (K); Morghak, *Furse 7735* (K). IRAN. Bam, *Leonard 6052* (K); Kerman, *Parris 75405* (E); Rudak, [= Dehbarek], *Davis & Bokhari D. 56505* (E). IRAQ. Hamah, *Karin & Noori 39981* (K); Tell Kotchek-Senonal, Mosul-Liwa, *J. B. Gillet 10846* (K); Southern Desert, S. of Al Salman, *Ravi, Agnew & Haines 1656* (E); Shaikhiya, Salma-Samawa, *Al-Shehbaz s.n.* (RNG). ISRAEL. Gilboa mountain, *Davis 4668* (E). JORDAN. Jordan *M.E.D.P. S/1113* (K). PAKISTAN. Chitral, Tirich, *Stainton 2780* (E). SAUDI ARABIA. Rumah, *White 73* (K). YEMEN. Huth, *Miller 3156* (E); Sanaa, *Miller 3401* (E).

8d. Capparis sicula Veill. subsp. **mesopotamica** Inocencio, D. Rivera, Obón & Alcaraz, subsp. nov. TYPE: [Iraq] "Amara, 9 Sep. 1918, *W. Edgar Evans, M/100* (E)" (holotype, designated here, E!, specimen E 65908). Figure 7.

Indumentum trichomatibus brevioribus, 100–250 µm longis, et tenuioribus, 15–20 µm latis, internodiis aculeis ad basim tenuioribus, 0.1–0.2 cm, pedicelis brevioribus, 3–4.5 cm, a typo differt.

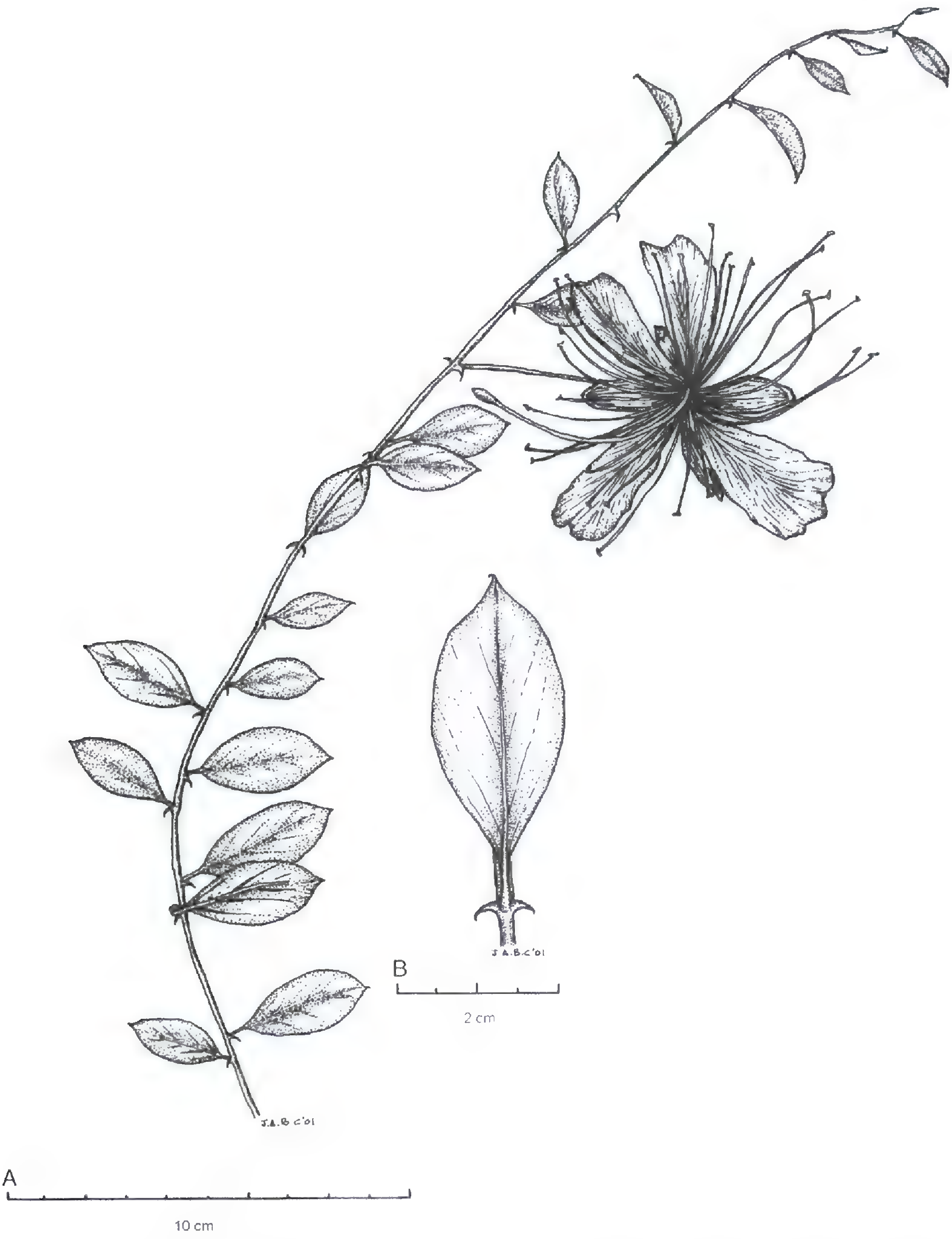

Figure 7. Details of the new subspecies *Capparis sicula* subsp. *mesopotamica* Inocencio, D. Rivera, Obón, & Alcaraz. —A. Stem and flower. —B. Detail of leaf and stipules. (A, B drawn by J.-A. Barreña from *Furse 9021*, K.)

Shrub procumbent; twigs straight, up to 2 m long, yellowish green; internodes 0.5–3.5 cm; stipules curved, retrorse, not decurrent, yellow-orange, 0.2–0.4 cm long, 0.1–0.2 cm wide at the base. Leaves obovate or oblong, 2.2–3.5 × 1.3–2.5 cm, herbaceous; indument very lax, trichomes thin and short, 100–250 × 15–20 μm; leaf veins prominent; base acute, apices acute or rounded; mucro long, 1–1.5 mm, straight; petioles short, 0.5–0.7 cm. Flower buds rounded or slightly acute; floral pedicels slender and short, 3–4.5 cm; flowers zygomorphic; abaxial (odd) sepal galeate, 1.2–1.8 cm long, 0.6–0.8 cm deep; stamens 100 to 150, anthers 2–2.5 mm, with acute apices. Fruit oblong, pulp red; ripe seeds brown, 2.8–3 × 2.4–2.8 × 1.7–2 mm.

Illustrations. Townsend & Guest (1980: pl. in front of the title page).

Phenology. Flowering and fruiting from July to September.

Distribution and habitat. Irano-Turanian Region. Extending somewhat into the Mediterranean and Saharo-Arabian Regions. Middle East [Iran, Iraq, Israel, Syria]. Sandstone, often near orchards and groves, at elevations from 0 to 2300 m.

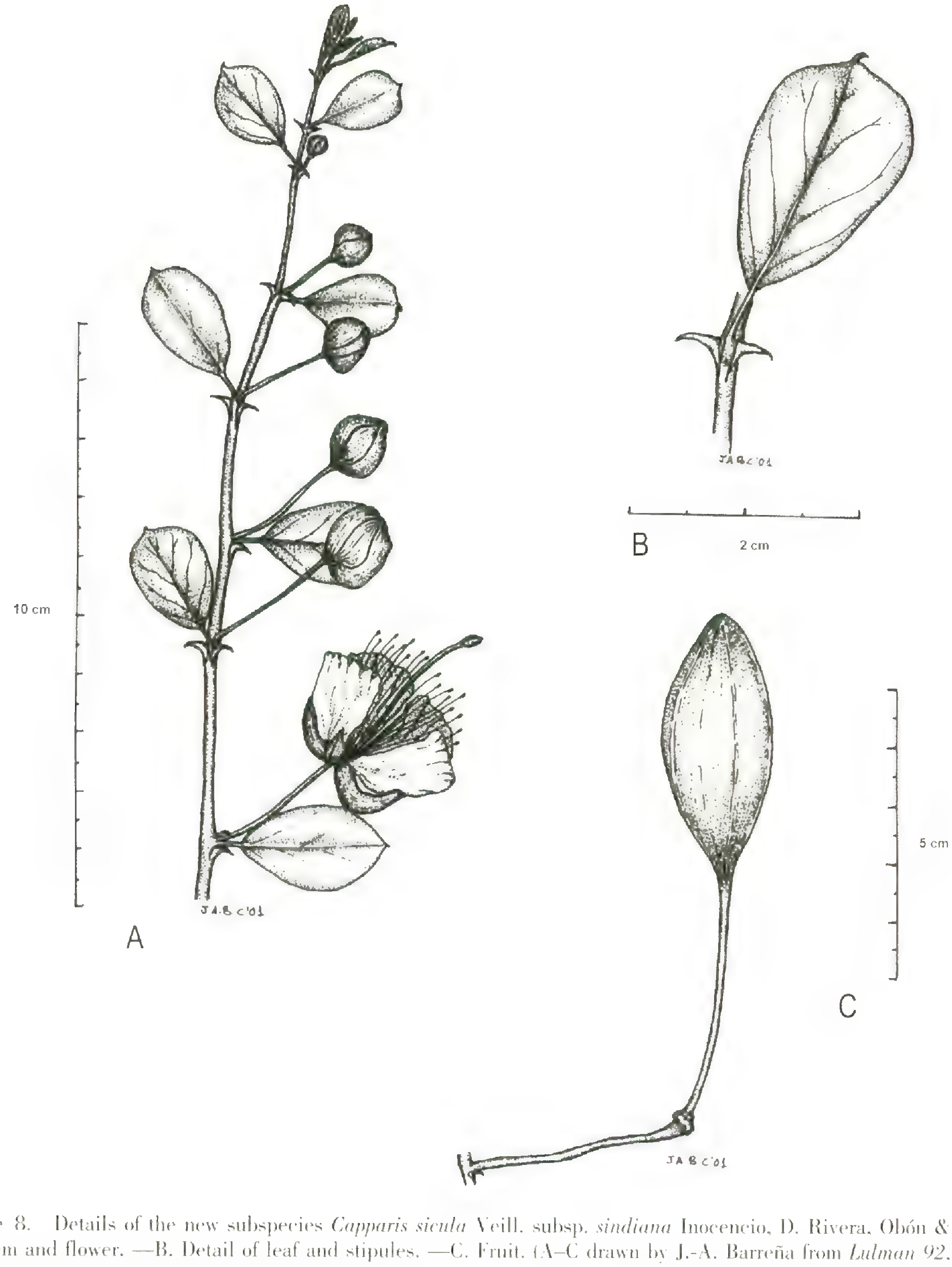

Figure 8. Details of the new subspecies *Capparis sicula* Veill. subsp. *sindiana* Inocencio, D. Rivera, Obón & Alcaraz. —A. Stem and flower. —B. Detail of leaf and stipules. —C. Fruit. (A–C drawn by J.-A. Barreña from *Lulman 92*, K.)

Paratypes. IRAN. Gulestan, *Furse 9021* (K); Másjed-e-Saleyman, *Lee 68* (K); Mazanderan, Tehran, *s.n. 10530* (E). IRAQ. Amara, *Edgar Evans M/100* (E); Saádiya, *Al-Kaisi 12894* (K); Sirk, Garmah, *R. Wheeler 322* (E). ISRAEL. Mizde Dragot, Dead Sea, *Danin & Knees 342* (RNG). SYRIA. Ain Dara, *Rivera & Obón s.n.* (MUB).

8e. Capparis sicula Veill. subsp. **sindiana** Inocencio, D. Rivera, Obón & Alcaraz, subsp. nov. TYPE: [Afghanistan] Barak, 26 Aug. 1986, *Mr. Lulman, 92* (holotype, K!). Figure 8.

Capparis oborata Royle, Illinois Bot. Himal. Mts. Vol. I: 73. 1839. TYPE: [Himachal Pradesh, India] "Hab. Hango [Chango] in Kunawur [Kinnaur, Kinawur]" (type not seen).

Caulibus viridescentibus vel luteis, trichomatibus laxis, pedunculis floralibus gracillimis brevioribus, a typo differt. Stipulis aureis, antheris minutis a subspecies mesopotamica differt.

Shrub procumbent, almost glabrous; twigs straight, sometimes reaching up to 3 m long, light green or yellowish; internodes 1–3 cm; stipules curved or somewhat curved, retrorse, occasionally spreading, not decurrent to somewhat decurrent, golden yellow contrasting with the twigs, 0.1–0.4 cm long, 0.1–0.2 cm wide at the base. Leaves obovate or elliptical, 1–3.5 × 1–3 cm, herbaceous; leaf veins prominent; base rounded, apices acute; mucro very small,

0.1–0.5 mm, straight or slightly curved; petioles short, 0.3–1 cm. Flower buds acute; floral pedicels slender, short, 1.5–4 cm; flowers zygomorphic; abaxial (odd) sepal galeate, 0.8–1.2 cm long, 0.4–0.6 cm deep; stamens 100 to 150, anthers 1.6–2 mm, with acute apices. Fruit ellipsoidal to oblong, pulp red; ripe seeds dark brown, 2.8–2.6 × 2.4–2.6 × 1.8–2 mm.

Illustrations. Royle (1839: 73); Narvi & Ali (1973: 8, fig. 2a); Polunin & Stainton (1984: pl. 16, n. 161).

Phenology. Flowering from July to September.

Distribution and habitat. Sudano-Zambezian, Indian and Irano-Turanian Regions. Middle East into India [Afghanistan, India, Pakistan]. Walls, meadows, and human dwellings; from 1000 to 3000 m.

In the lower left-hand part of the sheet with the holotype of *Capparis sicula* Veill. subsp. *sindiana* at K is a label with the following script: "FLORA OF AFGHANISTAN N . 92 / Name. *Capparis spinosa* L. / Native Name: Barak: dry riverbed. shale / Locality & Altitude: / sunny widespread growth. straggling. / Notes: procumbent stems. Fruit when ripe / dehisces along 3 lines to open out as / mass of bright red sticky fluid seeds / embedded in latter / alt. 1430 m. / Collector: Mr Lulman / Date: 26.8.1968."

The John Forbes Royle Herbarium is at LIV; however, Donna Young (pers. comm.) has checked in the Roylean herbarium and verified that no type specimen for *Capparis ovata* is there. Other herbaria where possible original material may be (DD and K) were unsuccessfully contacted. Therefore a neotype is neccessary.

Paratypes. AFGHANISTAN. Barak, *Lulman 92* (K). INDIA. Wangtu to Sholtu, Cholto bridge, Bashahr, Punjab, *Lace 178* (E); Li, Bushahr, Simla, Eastern Punjab, *Parmanand 725* (E). PAKISTAN. Balti, Iskalkoo, *Winterbottom s.n.* (K); Gaud nullah, Gupis, Gilgit, Karachi, *Omer 266* (E); Gilgit-Karimabad, 1500 m, *Qaiser, Omer & Husain 8444* (RNG); Kharipur, *Jafri 2421* (E); Shardu, Baltistan, *Shah 249* (E); above the Indus river, Shardu, Kashmir, Baltistan, 2600 m, *Webster & Nasir 5771* (K).

9. Capparis spinosa L., Sp. pl.: 503. 1753. TYPE: [France?] "Habitat in Europae australis arenosis, ruderatis" (lectotype, designated by Burtt & Lewis in Kew Bull. 4: 299. 1949, BM, Herb. Clifford: 203!, *Capparis* No. 912.348–50, validated by Jacobs, Blumea 12/3: 417. 1965).

Capparis peduncularis Presl., Delic. Prag.: 20–21. 1822.

Shrub procumbent; twigs straight, sometimes reaching up to 3 m, dark green; internodes 1.5–3.5 cm; stipules curved, retrorse, not decurrent, slender, weak or vestigial, rarely strong, usually very long and thin, dark yellow, 0.3–0.6 cm long, 0.1–0.2 cm wide at the base. Leaves ovate or obovate, 4–5 × 2.5–3.5 cm, herbaceous; indument very lax, trichomes thick and long, 25–40 × 300–500 μm, early falling; leaf veins not prominent; base rounded or somewhat tapering, apices acute; mucro very small, 0.1–0.5 mm, straight; petioles short, 0.7–1 cm. Flower buds acute; floral pedicels thick and long, 5–6.5 cm; flowers zygomorphic; abaxial (odd) sepal galeate, 1.8–2.4 cm long, 0.6–1.1 cm deep; stamens 100 to 150, anthers 2.5–2.8 mm, with acute apices. Fruit oblong, pulp red; ripe seeds brown, 3–3.2 × 2.6–2.8 × 2–2.5 mm.

Illustrations. Coste (1900: 142); Woodville (1794: plate 228, drawn and engraved by James Sowerby).

Phenology. Flowering from May to October.

Distribution and habitat. Mediterranean Region. Mediterranean Europe, Middle East into Turkey [France, Greece, Italy, Spain, Turkey]. Cultivated, sometimes found in secondary habitats as a feral or living among the parental species, at elevations from 0 to 250 m. Figure 2.

Rivera et al. (2006) reviewed the status and typification of *Capparis spinosa*. In summary, morphological, reproductive, and molecular data suggest, but do not prove, that this is a hybrid species kept in cultivation. The origins of the different populations are related to the coincidence of wild and/or cultivated individuals in proximity, belonging to *C. sicula* and *C. orientalis*, especially in the Western Mediterranean [Sicily, Mallorca], but also in Greece. The diversity within this crop shows a pattern of variation intermediate between the putative parentage (Rivera et al., 1999).

Selected specimens examined. FRANCE. Montpellier, *Bentham 243* (E); s.l. Agardh. *s.n.* (C). GREECE. Rhodes, *Sandermann s.n.* (C); Periol Botanical Garden (unknown), *Lasfeu s.n.* (C). ITALY. Sicily, Agrigento, *Davis 40229* (RNG); Stromboli, *B. Larsen s.n.* (C). SPAIN. **Alicante:** El Campello, *Inocencio & Alcaraz s.n.* (MUB); Paraiso Beach, Villajoyosa, *Hewat H 1040* (RNG). **Barcelona:** Barcelona, *Sennen 1587* (RNG). **Cordoba:** El Templete, *C. López CL1971/86* (RNG). **Mallorca:** Banyalbufar, *Inocencio & Alcaraz s.n.* (MUB); Campanet Caves, *Inocencio & Alcaraz s.n.* (MUB); from Santa Maria to Inca, *Inocencio & Alcaraz s.n.* (MUB); Valldemosa, *Christensen 1372* (C). TURKEY. Denizli, *Hänel 00.437* (E); Eskisehir-Sündihen, *Ehim 373* (E).

10. Capparis zoharyi Inocencio, D. Rivera, Obón & Alcaraz, sp. nov. TYPE: [Spain] "El Llano del Beal, Murcia, Spain, 7 July 1999, *Inocencio 42689*" (holotype, designated here, UMH!; paratypes, *Inocencio & Alcaraz 70102, 70103, 48689*, sent to K, E, and MO!). Figure 9.

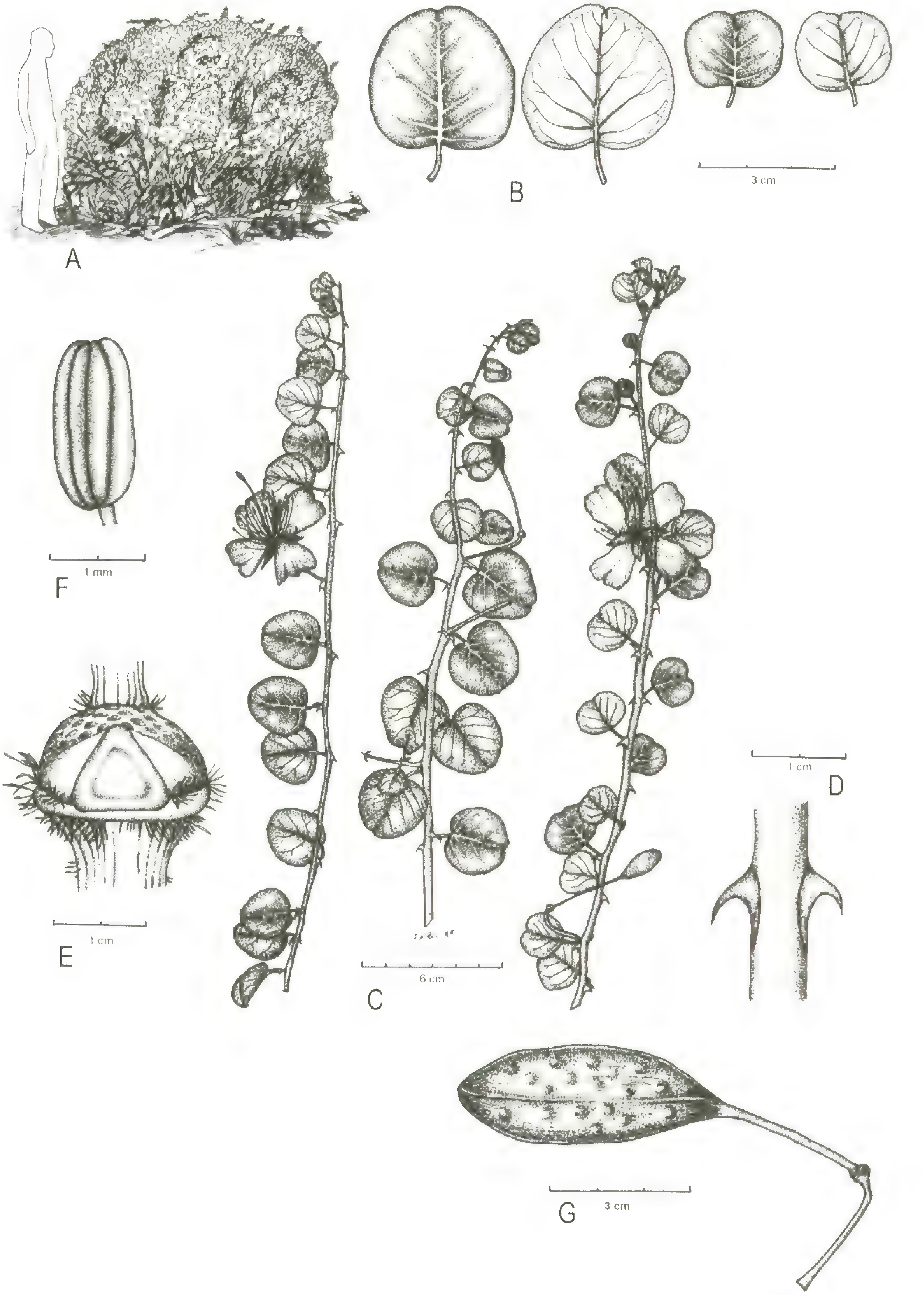

Figure 9. Details of the new species *Capparis zoharyi* Inocencio, D. Rivera, Obón & Alcaraz. —A. Habit. —B. Detail of leaf variability. —C. Stems. —D. Detail of the stipules. —E. Detail of nectary. —F. Detail of anther. —G. Fruit. (A–G drawn by P. Perales & J.-A. Barreña from *Inocencio & Alcaraz 18689*.)

Frutices erecti, usque ad 2 m; stipulis decurrentibus, similibus rosaris; foliis rotundis–obcordatis, rarius ovatis, (2–4 cm longis, 2–4 cm latis), apice emarginatis vel obtusis a *Capparis aegyptia* differt. In memoriam Michaelis Zohary dicata.

Shrub erect, glabrous; twigs straight, ± erect, up to 2 m long, green to reddish purple, older twigs bluish due to a waxy covering; internodes 1–5 cm; stipules curved, retrorse, strongly decurrent, rose type, orange, 0.3–0.6 cm long, 0.3–0.4 cm wide at the base. Leaves rounded to obcordate, rarely ovate, 2–4 × 2–4 cm, somewhat fleshy; leaf veins not prominent; base rounded, sometimes cordate, apices rounded or slightly obcordate; mucro absent or very small, 0.1–0.5 mm; petioles short, 0.7–1 cm. Flower buds rounded; floral pedicels thick and long, 3–5 cm; flowers slightly zygomorphic; abaxial (odd) sepal slightly galeate, 1.5–1.7 cm long, 0.6–0.9 cm deep; stamens 30 to 80, anthers 1.3–1.5 mm, with round apices. Fruit oblong, pulp yellow; ripe seeds brown, 3.4–3.8 × 3–3.2 × 2–2.2 mm.

Illustrations. Figure 14 in Zohary (1966: 358).

Phenology. Flowering and fruiting from March to October.

Distribution and habitat. Mediterranean Region. Mediterranean Europe, North Africa, Middle East into Turkey [Algeria, Egypt, Greece, Israel, Jordan, Lebanon, Morocco, Spain, Syria, Turkey]. Walls, rocks, pronounced slopes, at elevations from 0 to 200 m, often in the vicinity of human dwellings. Figure 4.

Paratypes. ALGERIA. Chiffa, Blida, *Davis 59527* (E). EGYPT. S.l., *N. Tadmor & A. Shmida S-420* (E); Sinai, *Boré 273* (K). GREECE. Samos, *W. Barbey 653* (E). SPAIN. **Murcia:** El Llano del Beal, *Alcaraz, Rivera & Obón 48733* (MUB). ISRAEL. Ein Gedi, *O. B. Lyschede 9/99/71* (C); Kfar Gileh y Manara, *Curle 65* (K); Manara, *C. M. Curle 143* (E); Mount Gilboa, *Davis 4667* (E); Wadi Qelt, *Davis 3651* (E); Wadi Yarmuk, *Davis 4604* (E). JORDAN. South of Rum Rest House, *Jallad et al. 7636* (E); Wadi Mujib, Ma'daba, *L. Boulos 5856* (K). LEBANON. Beirut, *s.n.* (E). MOROCCO. Safi, 20 June 1999, *Inocencio 60025* (MUB). SYRIA. Ain Dara, *Rivera & Obón 60049* (MUB); Damascus, *Rivera & Obón 60048* (MUB); Maaraba, *Rivera & Obón 60046* (MUB); Palmyra, *Rivera & Obón 60051* (MUB); Ugarit, *Rivera & Obón 60045* (MUB). TURKEY. Adana, *E. K. Balls 119* (E); Alanya, *Baytop 9701* (E); Antalya, *Smith 4* (K).

Discussion

This paper introduces changes in the *Capparis* sect. *Capparis* taxonomy adopted by authors such as Zohary (1960), who organized the diversity within this section around two core species, viz. *Capparis spinosa* and *C. ovata*. Most of the endemic taxa that previously were subordinated to one or the other of the above species at the rank of variety or subspecies have been here recognized as species or subspecies. One of the reasons for the synthetic approach of Jacobs (1965) or Zohary (1960) is the relative frequency of intermediate individuals in herbarium specimens that obscure the clear distinction among species. We refer to most of these as hybrid individuals, as revealed by our fieldwork in the Iberian Peninsula and North Africa (Inocencio, 2001).

Hybrids have been reported from different areas in which presumably hybrid swarms occur between two different *Capparis* species growing together. Hybrids are frequent in Iraq and neighboring countries of the Near East (Blakelock & Townsend, 1980), shadowing the distinction between species. The most relevant interspecific hybrid, for its economic uses, is *C. spinosa*, which is also the type "species" of the genus. It occurs spontaneously in populations of *C. orientalis* growing close to those of *C. sicula* in the western Mediterranean (Inocencio, 2001). Only this nothotaxon has been widely taken into cultivation. There have been no reported intersectional hybrids within *Capparis* subgenus *Capparis*, although *Capparis ovata* subsp. *myrtifolia* seems to be an intermediate between *C. ovata* subsp. *ovata* and *C. inermis* and, therefore, presumably their hybridogen. *Capparis ovata* is here restricted to the Algerian type and those populations closely related in morphology that extend from Morocco to Chad.

The large complex of Mediterranean and Irano-Turanian taxa formerly subordinated to *Capparis spinosa* is here combined under *C. sicula* because this is the name available according to the principle of priority.

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THE CARDUEAE (COMPOSITAE) REVISITED: INSIGHTS FROM ITS, *trn*L-*trn*F, AND *mat*K NUCLEAR AND CHLOROPLAST DNA ANALYSIS[1,2]

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Abstract

The new outline of relationships in basal branches of the family Compositae Giseke confirms that the sister group to the tribe Cardueae Cass. are not Mutisieae Cass., but rather a group of African genera now classified as the tribe Tarchonantheae Kostel. This change implies that the monophyly of the Cardueae must be reassessed on a molecular basis. Moreover, new collections in recent years allow us to extend our sampling to 70 of the 74 genera of the tribe. We performed a new molecular study of the tribe using one nuclear region (ITS) and two chloroplastic markers (*trn*L-*trn*F and *mat*K) in addition to a more appropriate outgroup. Our results confirm that the Cardueae is a natural group but indicate some changes in subtribal delineation: the subtribe Cardopatiinae Less. is recognized and some genera are moved to other subtribes (*Myopordon* Boiss., *Nikitinia* Iljin, *Syreitschikovia* Pavlov, and the *Xeranthemum* L. group). A recapitulation of a number of interesting questions that remain unresolved in the classification of some large genera is presented.

Key words: Cardueae, Compositae, genus delineation, ITS, *mat*K, phylogeny, tribal delimitation, *trn*L-*trn*F.

Resumen

El nuevo esquema de las relaciones en las ramas basales de la familia Compositae Giseke ha confirmado que el grupo hermano de la tribu Cardueae Cass. no es la tribu Mutisieae Cass., sino más bien un grupo de géneros africanos que ahora se clasifican como tribu Tarchonantheae Kostel. Este cambio implica que la monofilia de las Cardueae establecida sobre bases moleculares debe confirmarse. Además, nuestras nuevas recolecciones en los últimos años hacen que nuestro muestreo se extienda a 70 de los 74 géneros de la tribu. Hemos llevado a cabo un nuevo estudio molecular de la tribu usando una región nuclear (ITS) y dos cloroplásticas, además de seleccionar un grupo externo más adecuado. Nuestros resultados confirman que las Cardueae son un grupo natural, pero aconsejan algunos cambios en la delimitación subtribal: el reconocimiento de la subtribu Cardopatiinae Less. y el cambio de algunos géneros a otras subtribus (*Myopordon* Boiss., *Nikitinia* Iljin, *Syreitschikovia* Pavlov y el grupo *Xeranthemum* L.). Presentamos también una recapitulación sobre ciertas cuestiones interesantes que quedan sin resolver en la clasificación de algunos grandes géneros.

Introduction

Overview of Compositae Systematics

The systematics of Compositae is marked by three milestones, each one involving deep changes in the classification of the family. Since the history of this classification has been revised in depth in Funk et al. (2005), here we give only a short summary. The first attempt to classify Compositae was made by Cassini (1819), who defined 20 tribes. A more synthetic system was proposed by Bentham (1873) and, soon after, Hoffmann (1894). Both authors proposed a classification of two subfamilies and 16 tribes that gained general acceptance until very recently. The two latest revisions of the family, toward the end of the 20th century (Dittrich, 1977; Bremer, 1994), followed Hoffmann's classification. The third set of large-scale changes was produced by the introduction of methods based on DNA analysis. First came the pioneering study by Jansen & Palmer (1987) using cpDNA restriction site polymorphisms, which led to the description of a third subfamily, Barnadesioideae (Benth. & Hook. f.) K. Bremer & R. K. Jansen; this proposal was reflected in Bremer (1994). Second, the

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Table 1. Outline of two different proposals of classification of Compositae (only basal branches).

BREMER (1994)	PANERO & FUNK (2002)
BARNADESIOIDEAE (Benth. & Hook. f.) K. Bremer & R. K. Jansen	BARNADESIOIDEAE (Benth. & Hook. f.) K. Bremer & R. K. Jansen
• BARNADESIEAE D. Don	• BARNADESIEAE D. Don
CICHORIOIDEAE Chevall.	Stifftioideae clade (provisional)
• MUTISIEAE Cass.	• Stifftieae clade (provisional) (S. AMERICA, AFRICA)
• CICHORIEAE Lam. & DC.	MUTISIOIDEAE (Cass.) Lindl.
• CARDUEAE Cass.	• MUTISIEAE Cass. (S. AMERICA)
• VERNONIEAE Cass.	GOCHNATIOIDEAE (Benth. & Hook. f.) Panero & V. A. Funk
• LIABEAE Rydb.	HECASTOCLEIDOIDEAE Panero & V. A. Funk
• ARCTOTEAE Cass.	• HECASTOCLEIDEAE Panero & V. A. Funk
ASTEROIDEAE (Cass.) Lindl.	CARDUOIDEAE Cass. ex Sweet
.... (3 subfamilies, 17 tribes)	• DICOMEAE Panero & V. A. Funk
	• TARCHONANTHEAE Kostel.
	• CARDUEAE Cass.
	.... (11 subfamilies, 36 tribes)

latest and more revolutionary study by Panero & Funk (2002) analyzed sequences of nine chloroplast regions across the entire family and proposed a new classification with 11 subfamilies and 35 tribes; this was in some ways closer to Cassini's analytical views than to synthetic approaches. The dramatic differences between Bremer's (1994) and Panero and Funk's (2002) classification are illustrated in Table 1 (only the basal groups are shown). The high statistical support for the latter and its sound correlation with morphology leads us to believe that the new classification of Compositae is near to being definitive.

THE TRIBE CARDUEAE

Cardueae Cass. is one of the largest tribes of Compositae, with ca. 2500 species. Previous studies based on DNA sequence analyses, both nuclear (Susanna et al., 1995) and combined chloroplast and nuclear (Garcia-Jacas et al., 2002), confirm Cardueae as monophyletic. However, the new classification shows that our previous outgroup choice was not the best choice. In the classic system of Compositae (e.g., Heywood et al., 1977; Bremer, 1994), Cardueae were classified in subfamily Cichorioideae Chevall., close to tribes Cichorieae Lam. & DC. and Mutisieae Cass. (Table 1). Therefore, in our first nuclear-DNA-based phylogeny (Susanna et al., 1995), the outgroup was composed of one Cichorieae (*Tragopogon* L.) and three Mutisieae (*Ainsliaea* DC., *Gerbera* L., and *Warionia* Benth. & Coss.). In Garcia-Jacas et al. (2002), we replaced *Ainsliaea*, *Tragopogon*, and *Warionia* because of the increasing difficulties in aligning the ITS region, and we used two Mutisieae as outgroups, *Gerbera* and *Mutisia* L. f. However, according to the new classification by Panero & Funk (2002), tribe Cichorieae (*Tragopogon*) is derived in relation to Cardueae; *Ainsliaea* and *Warionia* do not belong to Mutisieae but to Pertyeae Panero & V. A. Funk and Gundelieae H. Rob. & Brettell, respectively, both tribes also derived with regard to Cardueae; and *Gerbera* and *Mutisia* are placed in Mutisieae sensu stricto, phylogenetically far from Cardueae (Table 1). With these outgroup species, Cardueae will always be monophyletic, and monophyly of the tribe has always been a controversial issue. The outgroup should be chosen from the clade formed by tribe Tarchonantheae plus the genus *Oldenburgia* L., a clade that appears as the true sister group to Cardueae with bootstrap support values of 100% in Panero and Funk (2002). In fact, Cardueae, Dicomeae Panero & V. A. Funk, and Tarchonantheae (plus *Oldenburgia*) compose a monophyletic subfamily, Carduoideae Cass. ex Sweet, also with the highest statistical support (Panero & Funk, 2002). Morphological connections between Cardueae and the rest of subfamily Carduoideae are, however, unknown to date.

TRIBAL LIMITS OF CARDUEAE

In the earliest classification (Cassini, 1819), present Cardueae were divided in three tribes: Echinopeae, Carlineae, and Cardueae, the latter with two subtribes: Carduinae and Centaureinae. Bentham (1873) and Hoffmann (1894) proposed grouping the three tribes in a single tribe Cardueae that held four subtribes: Echinopinae (Cass.) Dumort., Carlininae (Cass.) Dumort., Carduinae Cass., and Centaureinae (Cass.) Dumort. This was a conservative approach that was generally accepted for a very long time. However, discussion on the status of Echinopinae restarted when Wagenitz (1976) proposed the segregation of the

subtribe as a separate tribe, Echinopeae. Dittrich (1977) returned to Cassini's early views and proposed the restoration of Echinopeae and Carlineae. Finally, Bremer (1994) reintroduced the conservative approach with only one tribe, Cardueae, which, according to our molecular studies, is a better solution (Susanna et al., 1995; Garcia-Jacas et al., 2002).

SUBTRIBAL CLASSIFICATION

Within Cardueae, there is general agreement in accepting four groups, regardless of the rank (tribe or subtribe) adopted. Three subtribes are natural (Carlininae, Echinopinae, and Centaureinae) and the fourth (Carduinae) is a paraphyletic assemblage (Garcia-Jacas et al., 2002).

Subtribe Carlininae is sister to the rest of the tribe. A striking and probably plesiomorphic character is the presence of true ray florets in at least one genus of Carlininae, *Atractylis* L., while remaining subtribes have only disk florets. Capitula are usually subtended by pectinate-pinnatisect leaf-like bracts; corolla lobes are very short, only 1–3 mm long; and the pappus has long, plumose bristles, often connate at the base forming broader, robust scales (Susanna & Garcia-Jacas, in press).

Subtribe Echinopinae is easily characterized by its second-order inflorescences (uniflowered capitula clustered in a large synflorescence). Our latest molecular phylogeny indicates that Echinopinae should also include the genera of the *Xeranthemum* group and we previously proposed that the small heads of the genus *Xeranthemum* and allies could be interpreted as reduced synflorescences (Garcia-Jacas et al., 2002).

Subtribe Carduinae is a paraphyletic complex of genera with some well defined groups (*Arctium* L. group, *Onopordum* L. group, *Saussurea* DC. group, or the thistles) together with genera of problematic ascription like *Berardia* Vill. or *Staehelina* L. All the genera of Carduinae have basal or basal-abaxial insertion areole of achenes and, usually, a simple pappus, and are often spiny.

Finally, subtribe Centaureinae is the most derived group and is characterized by achenes with lateral-adaxial insertion areole, a double pappus, and, with few exceptions, unarmed leaves. However, examining the limits between Carduinae and Centaureinae represents a challenge, because differences lie in microcharacters of the achene and pappus that are difficult to observe in incomplete or immature herbarium materials. The examples of *Nikitinia* and *Syreitschikovia* illustrate these difficulties (Susanna et al., 2002) and the ascription of these and other genera should be checked against a molecular phylogeny.

In Garcia-Jacas et al. (2002) we suggested that maybe a fifth subtribe could be recognized, Cardopatiinae Less., with two genera: *Cardopatium* Juss. and *Cousiniopsis* Nevski. Cardopatiinae were placed in an intermediate position between Carlininae and the rest of the tribe (Garcia-Jacas et al., 2002). However, we have postponed the restoration of this subtribe until more unambiguous evidence has been collected.

GENERIC LIMITS IN TRIBE CARDUEAE

Other points of interest are genus affinities and limits in Cardueae, a tribe with some of the largest genera of the family. Regarding genus affinities, on the basis of morphology and partial molecular studies, the two largest subtribes (Carduinae and Centaureinae) were subdivided into informal groups (Susanna & Garcia-Jacas, in press), which should be checked against a more comprehensive molecular phylogeny. As to genus limits, in our latest revision of Cardueae (Susanna & Garcia-Jacas, in press) we adopted a broad generic concept for *Cousinia* Cass. (600 species), *Jurinea* Cass. (200), and *Saussurea* (400) because of the lack of recent systematic revisions for all three. Recently, on the basis of a partial study of DNA sequences and achene morphology, Raab-Staube (2003) proposed the restoration of two small genera, *Frolovia* (DC.) Lipsch. and *Lipschitziella* Kamelin, and described a new genus, *Himalaiella* Raab-Staube, all of these within the *Saussurea* group.

SCOPE AND AIMS

With the addition of new materials, our DNA sampling covers 70 of the 74 accepted genera of Cardueae: only *Ancathia* DC. (Carduinae, Central Asia), *Centaurodendron* Johow (Centaureinae, Juan Fernández archipelago), *Goniocaulon* Cass. (Centaureinae, India and East Tropical Africa), and *Takeikadzuchia* Kitag. & Kitam. (Carduinae, Mongolia) are absent. However, the position of these within the tribe and their subtribal ascription has never been challenged on a morphological basis (Susanna & Garcia-Jacas, in press). To test our broad generic concept, we included the genera *Frolovia*, *Lipschitziella*, and *Modestia* Kharadze & Tamamsch., which we submerge in *Jurinea*; and *Anura* (Kult.) Tscherneva and *Tiarocarpus* Rech. f., which we had previously considered in *Cousinia* (Susanna & Garcia-Jacas, in press). We also included the published sequence of the recently described genus *Himalaiella*. For this wide representation of Cardueae, we completed the ITS and *mat*K regions and, in view of the low resolution of basal groups in previous analyses, we added a new marker. Low resolution in

many molecular phylogenies may be solved by adding more data to DNA sequence matrices as discussed in Panero & Funk (2002). We used a chloroplast marker, the *trn*L-*trn*F intergenic region, which is widely utilized in Compositae (Bayer & Starr, 1998; Liu et al., 2002; Oberprieler, 2002; Panero & Funk, 2002). Our goals were to:

(a) verify monophyly of Cardueae using species from the sister clade Tarchonantheae and *Oldenburgia* as an outgroup;
(b) clarify subtribal classification and define the position of Cardopatiinae, which might constitute a fifth subtribe;
(c) examine whether the informal species groups defined in subtribes Carduinae and Centaureinae are natural, and check the systematic position within these groups of genera not included in our previous studies; and
(d) verify the suitability of a broad generic concept in certain large genera of Cardueae by analyzing species from genera that we had previously rejected on the basis of morphological characters.

Material and Methods

Plant Material

Sampling was defined on the basis of Garcia-Jacas et al. (2001), Garcia-Jacas et al. (2002), Susanna et al. (2003), and Susanna & Garcia-Jacas (in press), in order to represent most of the genera of tribe Cardueae. Thirteen accepted genera (*Amphoricarpos* Vis., *Karvandarina* Rech. f., *Lamyropappus* Knorring & Tamamsch., *Lamyropsis* (Kharadze) Dittrich, *Myopordon* Boiss., *Nikitinia*, *Olgaea* Iljin, *Plagiobasis* Schrenk, *Polytaxis* Bunge, *Russowia* C. Winkl., *Syreitschikovia*, *Siebera* J. Gay, *Tricholepis* DC., and *Tugarinovia* Iljin) are sequenced here for the first time. Six other genera that were not accepted in our latest revision of the tribe (Susanna & Garcia-Jacas, in press) are *Aegopordon* Boiss., *Anura*, *Frolovia*, *Lipschitziella*, *Modestia*, and *Tiarocarpus*. Two more genera, *Dolomiaea* DC. and *Himalaiella*, were obtained from sequences published elsewhere. Three outgroup species were chosen, two among Tarchonantheae and another from the genus *Oldenburgia*, because the tribe and the genus form the sister clade to Cardueae (Panero & Funk, 2002). Many of our ITS1 and ITS2 sequences from previous studies (Garcia-Jacas et al., 2001, 2002) have been completed with the sequence of the 5.8 S gene, and some of our old manual ITS sequences (Susanna et al., 1995) were re-sequenced or confirmed by automatic sequencing. Both previously published (Garcia-Jacas et al., 2002) and new sequences of the *mat*K gene were used in this analysis. All the *trn*L-*trn*F sequences analyzed are new, with the exception of *Dolomiaea* (from Liu, unpublished) and some species of *Saussurea* (from Raab-Staube, 2003). The number of new sequences is 283 for a total of 466. The origin of the samples and their GenBank accession numbers are given in Table 2.

DNA Extraction, Amplification, and Sequencing

Total genomic DNA was extracted following the miniprep procedure of Doyle & Doyle (1987) as modified by Soltis et al. (1991) and Cullings (1992), from silica gel-dried leaves collected in the field or from fresh leaves of plants cultivated in the Botanic Institute of Barcelona. In some cases, herbarium material was used.

cpDNA *trn*L-*trn*F Region Strategies

The plastid *trn*L-*trn*F region includes the *trn*L intron, the 3′ *trn*L (UAA) exon, and the intergenic spacer between *trn*L (UAA) and *trn*F (GAA), that were amplified and sequenced together. Universal primers *trn*L-c, forward, and *trn*L-f, reverse (Taberlet et al., 1991), were used for amplifying the *trn*L-*trn*F region. In some cases, *trn*L-d, reverse, and *trn*L-e, forward, were used. Polymerase chain reaction (PCR) was conducted in a thermocycler (MJ Research PTC 100). The PCR procedure included a warm start at 95°C for 1 minute 35 seconds, followed by 80°C during which the polymerase (Ecotaq, Ecogen S.R.L., Barcelona, Spain) was added, with 34 cycles of 1 min. denaturation at 93°C, 1 min. annealing at 58°C, 1 min. extension at 72°C, and a final 10 min. extension at 72°C.

PCR products were cleaned with a QIAquick PCR Purification Kit (Qiagen Inc., Valencia, CA) and sequenced with the *trn*L-c and *trn*L-f primers. Direct sequencing of the amplified DNA segments was performed using the BigDye Terminator Cycle Sequencing v3.1 (PE Biosystems, Foster City, CA), following the protocol recommended by the manufacturer. Nucleotide sequencing was carried out at the Serveis Científico-Tècnics of the University of Barcelona on an ABI PRISM 3700 DNA analyzer (PE Biosystems, Foster City, CA).

cpDNA *mat*K Gene Strategies

We have sequenced the first 1000 base pairs at the 5′ end, because this part includes most of the variability in the *mat*K plastid gene (Hilu & Liang, 1997). Partial *mat*K was amplified by PCR with the primers *trn*K-710 F (Johnson & Soltis, 1995) and AST-1R (Garcia-Jacas et al., 2002). The PCR procedure included a warm start at 94°C for 1 min. 20 sec., followed by 80°C during which the polymerase (Ecotaq, Ecogen S.R.L., Barcelona, Spain) was

Table 2. Origin of the materials, herbaria where the vouchers are deposited, and GenBank accession numbers (new sequences are boldfaced).

Species	Voucher	ITS accession	*trn*L-*trn*F accession	*mat*K accession
Acantholepis orientalis Less.	Garcia-Jacas et al., 2002	**AY826222**	**AY772267**	**AY785086**
Acroptilon repens (L.) DC.	Garcia-Jacas et al., 2001	**AY826223**	**AY772268**	AY013489
Alfredia acantholepis Kar. & Kir.	Kazakhstan, *Susanna 2092 et al.* (BC)	**AY826224**	—	
Alfredia cernua (L.) Cass.	Garcia-Jacas et al., 2002	**AY826225**	**AY772269**	AY013519
Alfredia nivea Kar. & Kir.	Kazakhstan, *Susanna 2090 et al.* (BC)	**AY826226**	**AY772270**	**AY785087**
Amberboa turanica Iljin	Garcia-Jacas et al., 2001	AY012275, AY012311		
Amphoricarpos autariatus Blecic & Mayer	Serbia & Montenegro, *Stevanovic et al.* 1.10.91 (BC)	**AY826227**	**AY772271**	**AY785088**
Amphoricarpos exsul O. Schwarz	Turkey, *Susanna 2256 et al.* (BC)	**AY826228**	**AY772272**	**AY785089**
Arctium lappa L.	Garcia-Jacas et al., 2002	**AY826229**	**AY772273**	AY013520
Arctium minus Bernh.	Garcia-Jacas et al., 2002	**AY826230**	**AY772274**	AY013521
Atractylis cancellata L.	Garcia-Jacas et al., 2002	**AY826231**	**AY772275**	AY013522
Atractylis carduus (Forssk.) Christ.	Garcia-Jacas et al., 2002	**AY826232**	**AY772276**	AY013523
Atractylis humilis L.	Garcia-Jacas et al., 2002	AF319052, AF319106	—	
Atractylodes japonica Koidz. ex Kitam.	Garcia-Jacas et al., 2002	**AY826233**	**AY772277**	AY013524
Berardia subacaulis Vill.	Garcia-Jacas et al., 2002	**AY826234**	**AY772278**	AY013525
Brachylaena discolor DC.	South Africa, *Ortiz* 20.3.02 (NBG)	**AY826236**	**AY772280**	**AY785090**
Callicephalus nitens (M. Bieb. ex Willd.) C. A. Mey.	Garcia-Jacas et al., 2001	**AY826237**	**AY772281**	AY013492
Cardopatium corymbosum (L.) Pers.	Garcia-Jacas et al., 2002	**AY826238**	**AY772282**	AY013526
Carduncellus duranxii Batt. & Trab.	Vilatersana et al., 2000; Garcia-Jacas et al., 2001	**AY826239**	**AY772283**	AY013493
Carduncellus mareoticus (Delile) Hanelt	Vilatersana et al., 2000	AF140480, AF140481	—	—
Carduus carlinoides Gouan	Garcia-Jacas et al., 2002	**AY826240**	**AY772284**	AY013527
Carduus defloratus L.	Spain, *Garnatje 18* (BC)	**AY826241**	**AY772285**	AY785091
Carduus pycnocephalus L.	Garcia-Jacas et al., 2002	AF319111, AY013528	—	AY013528
Carlina acanthifolia All.	Garcia-Jacas et al., 2002	**AY826242**	**AY772286**	AY013529
Carlina falcata Svent.	Garcia-Jacas et al., 2002	**AY826243**	**AY772287**	AY013530
Carlina gummifera (L.) Less.	Garcia-Jacas et al., 2002	**AY826244**	**AY772288**	AY013531
Carlina lanata L.	Garcia-Jacas et al., 2002	**AY826245**	**AY772289**	AY013532
Carlina macrophylla (Desf.) DC.	Garcia-Jacas et al., 2002	AF319062, AF319116	—	—
Carlina vulgaris L.	Garcia-Jacas et al., 2002	**AY826246**	**AY772290**	AY013533
Carthamus creticus L.	Vilatersana et al., 2000	**AY826247**	**AY772291**	**AY785092**
Carthamus leucocaulos Sibth. & Sm.	Vilatersana et al., 2000	AF140460, AF140461	—	—
Carthamus oxyacantha M. Bieb.	Vilatersana et al., 2000; Garcia-Jacas et al., 2001	**AY826248**	**AY772292**	AY013494
Carthamus tinctorius L.	Vilatersana et al., 2000	AF140458, AF140459	—	
Carthamus turkestanicus Popov	Vilatersana et al., 2000	**AY826249**	**AY772293**	**AY785093**
Centaurea alba L.	Garcia-Jacas et al., 2000, 2001	**AY829446**	—	AY013495
Centaurea amadanensis Sch. Bip.	Garcia-Jacas et al., 2000	AF058839, AF058861	—	—

Table 2. Continued.

Species	Voucher	ITS accession	*trn*L-*trn*F accession	*mat*K accession
Centaurea behen L.	Garcia-Jacas et al., 2000, 2001	**AY826250**	**AY772294**	AY013496
Centaurea benedicta L.	France, Nancy Bot. Gard. (BC)	AF058850, AF058875	—	AY013508
Centaurea bruguierana (DC.) Hand.-Mazz.	Garcia-Jacas et al., 2000, 2001	**AY826251**	**AY772295**	AY013497
Centaurea calcitrapa L.	Egypt, *Susanna 1866 & Vilatersana* (BC)	**AY826252**	—	—
Centaurea carolipauana Fern. Casas & Susanna	Garcia-Jacas et al., 2001	**AY826253**	**AY772296**	AY013498
Centaurea cyanus L.	Spain, *Garcia-Jacas & Susanna 2076* (BC)	**AY826254**	—	—
Centaurea depressa M. Bieb.	Garcia-Jacas et al., 2001	**AY826255**	**AY772297**	AY013499
Centaurea involucrata Desf.	Susanna et al., 1995; Garcia-Jacas et al., 2001	**AY826256**	**AY772298**	AY013503
Centaurea kotschyi (Boiss. & Heldr.) Hayek	Garcia-Jacas et al., 2000	**AY829441**	—	—
Centaurea lagascana Graells	Garcia-Jacas et al., 2001	**AY826257**	**AY772299**	AY013504
Centaurea lingulata Lag.	Garcia-Jacas et al., 2000, 2001	**AY826258**	**AY772300**	AY013505
Centaurea linifolia L.	Garcia-Jacas et al., 2000	AF058832, AF058857	—	—
Centaurea macrocephala Muss.-Puschk.	Susanna et al., 1995	L35873	—	—
Centaurea montana L.	Susanna et al., 1995	L35887	—	—
Centaurea polyacantha Willd.	Susanna et al., 1995	L35878	—	—
Centaurea rhizantha C. A. Mey.	Garcia-Jacas et al., 2000	AF058842, AF058867	—	—
Centaurothamnus maximus Wagenitz & Dittrich	Garcia-Jacas et al., 2001	**AY826259**	**AY772301**	AY013506
Chardinia orientalis (L.) O. Kuntze	Garcia-Jacas et al., 2002	**AY826260**	**AY772302**	AY013534
Cheirolophus benoistii (Humbert) Holub	Susanna et al., 1999	AF045415, AF079942	—	—
Cheirolophus mauritanicus (Font Quer) Susanna	Susanna et al., 1999	**AY826261**	**AY772303**	AY013507
Cheirolophus sempervirens (L.) Pomel	Susanna et al., 1999	AF021156, AF021173	—	—
Cheirolophus teydis (C. Smith) G. López	Susanna et al., 1995	**AY826262**	**AY772304**	AY785094
Cirsium arvense (L.) Scop.	Susanna et al., 1995	L35867	—	—
Cirsium echinus (M. Bieb.) Hand.-Mazz.	Garcia-Jacas et al., 2002	**AY826263**	**AY772305**	AY013535
Cirsium ochrolepidium Juz.	Uzbekistan, *Susanna 2048 et al.* (BC)	**AY826264**	**AY772306**	**AY785095**
Cirsium palustre (L.) Scop.	Garcia-Jacas et al., 2002	**AY826265**	**AY772307**	AY013536
Cousinia alberti Regel & Schmalh.	Susanna et al., 2003	AY373721, AY373688	—	—
Cousinia arachnoidea Fisch. & C. A. Mey.	Susanna et al., 2003	AY373722, AY373689	—	—
Cousinia astracanica (Spreng.) Tamamsch.	Susanna et al., 2003	**AY826266**	**AY772308**	AY373670
Cousinia caespitosa C. Winkl.	Susanna et al., 2003	AY373724, AY373691	—	—
Cousinia canescens DC.	Garcia-Jacas et al., 2002	AF319068, AF319122	—	—

Table 2. Continued.

Species	Voucher	ITS accession	*trn*L-*trn*F accession	*mat*K accession
Cousinia chrysantha Kult.	Susanna et al., 2003	AY373725, AY373692	—	—
Cousinia congesta Bunge	Susanna et al., 2003	AY373726, AY373693	—	—
Cousinia coronata Franch.	Susanna et al., 2003	**AY826267**	**AY772309**	AY373662
Cousinia dissecta Kar. & Kir.	Susanna et al., 2003	AY373728, AY373695	—	—
Cousinia esfandiarii Rech. f. & Aellen	Garcia-Jacas et al., 2002	AF319069, AF319123	—	AY013537
Cousinia grandifolia Kult.	Susanna et al., 2003	**AY826268**	**AY772310**	AY373679
Cousinia karatavica Regel & Schmalh.	Susanna et al., 2003	AY373732, AY373699	—	—
Cousinia lappacea Bunge	Susanna et al., 2003	**AY826269**	**AY772311**	AY373677
Cousinia microcarpa Boiss.	Susanna et al., 2003	**AY826270**	**AY772312**	AY373667
Cousinia neubaueri Rech. f. [=*Tiarocarpus neubaueri* (Rech. f.) Rech. f.]	Afghanistan, *Dieterle 1410* (W)	**AY826271**	**AY772376**	**AY785096**
Cousinia onopordioides Ledeb.	Garcia-Jacas et al., 2002	AF319070, AF319124	—	
Cousinia pallidivirens Kult. [=*Anura pallidivirens* (Kult.) Tschern.]	Uzbekistan, *Botschantzev* 20.6.71 (LE)	**AY826272**	—	—
Cousinia platylepis Schrenk	Susanna et al., 2003	AY373737, AY373704	—	—
Cousinia polycephala Rupr.	Susanna et al., 2003	**AY826273**	**AY772313**	AY373668
Cousinia purpurea C. A. Mey.	Susanna et al., 2003	**AY826274**	**AY772314**	
Cousinia syrdariensis Kult.	Susanna et al., 2003	AY373741, AY373708	—	—
Cousinia tianshanica Kult.	Susanna et al., 2003	AY373743, AY373710	—	—
Cousinia triflora Schrenk	Susanna et al., 2003	**AY826275**	**AY772315**	AY373675
Cousinia umbrosa Bunge	Susanna et al., 2003	**AY826276**	**AY772316**	AY373676
Cousiniopsis atractyloides (C. Winkl.) Nevski	Garcia-Jacas et al., 2002	AF319071, AF319125	**AY772317**	**AY785097**
Crocodylium creticum (Boiss. & Heldr.) N. Garcia & Susanna	Garcia-Jacas et al., 2001 [as *Aegialophila cretica*(L.) Boiss. & Heldr.]	**AY826278**	**AY772318**	AY013490
Crocodylium pumilum (L.) N. Garcia & Susanna	Garcia-Jacas et al., 2001 [as *Aegialophila pumilio* (L.) Boiss. & Heldr.]	AY012272, AY012308	-	
Crocodylium syriacum Cass.	Garcia-Jacas et al., 2001 [as *Centaurea crocodylium* L.]	**AY826279**	**AY772319**	**AY785098**
Crupina crupinastrum (Moris.) Vis.	Susanna et al., 1995	L35884	—	—
Crupina vulgaris Cass.	Garcia-Jacas et al., 2001	**AY826280**	**AY772320**	—
Cynara cornigera Lind.	Garcia-Jacas et al., 2002	**AY826281**	**AY772321**	AY013538
Cynara humilis L.	Portugal, *Blanqué 8* (BC)	**AY826282**	**AY772322**	**AY785099**
Dolomiaea unp. sp. (*D. tibetica* in GenBank)	Liu (unpubl.)	AY366334	AY330342	—
Echinops niveus Wall.	Garnatje et al., 2005	AY538634	**AY772323**	**AY785100**
Echinops persicus Stev. & Fisch.	Garnatje et al., 2005	AY538639	**AY772324**	AY785101
Echinops ritro L.	Garcia-Jacas et al., 2002	AF319074, AF319128	—	
Echinops spinosissimus Turra	Garcia-Jacas et al., 2002	AF319075, AF319129	—	AY013539
Echinops tschimganicus B. Fedtsch.	Garnatje et al., 2005	AY538633	**AY772325**	**AY785102**
Echinops viscosus DC.	Garcia-Jacas et al., 2002	**AY826283**	**AY772326**	AY013540

Table 2. Continued.

Species	Voucher	ITS accession	*trn*L-*trn*F accession	*mat*K accession
Femeniasia balearica (J. J. Rodr.) Susanna	Garcia-Jacas et al., 2001	**AY826284**	**AY772327**	AY013509
Galactites tomentosa Moench	Garcia-Jacas et al., 2002	**AY826285**	**AY772328**	AY013541
Hypacanthium echinopifolium (Bornm.) Juz.	Susanna et al., 2003	**AY826286**	**AY772329**	—
Jurinea albicaulis Bunge	Susanna et al., 2003	**AY826287**	**AY772330**	AY373684
Jurinea berardioides (Boiss.) O. Hoffm.	Pakistan, *Rechinger 28456* (W) [as *Aegopordon berardioides* Boiss.]	**AY826288**	**AY772331**	—
Jurinea carduiformis Boiss.	Garcia-Jacas et al., 2002 [as *Outreya carduiformis* Jaub. & Spach]	**AY826289**	**AY772332**	**AY785103**
Jurinea humilis (Desf.) DC.	Susanna et al., 1995	L35868	—	—
Jurinea lanipes Rupr.	Susanna et al., 2003	AY373748, AY373715	—	—
Jurinea macrocephala DC.	Garcia-Jacas et al., 2002	AF319081, AF319135	—	—
Jurinea modesta Boiss. 2002 [=*Hyalochaete modesta* (Boiss.) Dittrich & Rech. f.]	Garcia-Jacas et al., 2002	AF319080, AF319134	—	—
Jurinea moschus (Habl.) Bobrov [=*Jurinella moschus* (Habl.) Bobrov]	Garcia-Jacas et al., 2002	AF319083, AF319137	—	—
Jurinea robusta Schrenk	Susanna et al., 2003	**AY826291**	**AY772333**	—
Jurinea sp. ined. 2 [= *Modestia darwasica* (C. Winkl.) Kharadze & Tamamsch.]	Tadjikistan, *Bubanov* 27.9.61 (LE)	**AY826290**	—	—
Jurinea sp. ined. 1	Garcia-Jacas et al., 2002	AF319082, AF319136	—	AY013543
Jurinea stoechadifolia (Bieb.) DC.	Ukraine, *Romo 10321 et al.* (BC)	**AY826292**	—	—
Jurinea suffruticosa Regel	Kazakhstan, *Susanna 2186 et al.* (BC)	**AY826293**	—	—
Karvandarina aphylla Rech. f., Aellen & Esfand.	Iran, *Soják 8379* (W)	**AY826294**	—	—
Klasea serratuloides (DC.) Greuter & Wagenitz	Garcia-Jacas et al., 2001	**AY826295**	**AY772334**	AY013514
Lamyropappus schakaptaricus (B. Fedtsch.) Knorr. & Tamamsch.	Kyrgyzistan, *Poljakov* 29.8.53 (LE)	**AY826296**	**AY772335**	**AY785104**
Lamyropsis cynaroides (Lam.) Dittrich	Turkey, *Susanna 2267 et al.* (BC)	**AY826297**	**AY772336**	**AY785105**
Leuzea conifera (L.) DC.	Garcia-Jacas et al., 2001	**AY826298**	**AY772337**	—
Mantisalca salmantica (L.) Briq. & Cavill.	Garcia-Jacas et al., 2001	AY012292, AY012328	—	—
Myopordon aucheri Boiss.	Iran, *Carls s.n.* (W)	**AY826299**	**AY772338**	—
Myopordon hyrcanum (Bornm.) Wagenitz	Iran, *Koelz 16395* (W)	**AY826300**	**AY772339**	—
Myopordon persicum Boiss.	Iran, *Remandieri s.n.* (W)	**AY826301**	—	—
Nikitinia leptoclada (Bornm. & Sint.) Iljin	Turkmenistan, *Markova* 3.8.54 (LE)	**AY829142**	—	—
Notobasis syriaca (L.) Cass.	Garcia-Jacas et al., 2002	**AY826302**	**AY772340**	AY013545
Oldenburgia intermedia Bond.	South Africa, *Ortiz* 3.4.02 (NBG)	**AY826303**	**AY772341**	**AY785106**
Olgaea baldschuanica (C. Winkl.) Iljin	Tadjikistan, *Kamelin et al.* 31.5.86 (LE)	**AY826304**	**AY772342**	**AY785107**

Table 2. Continued.

Species	Voucher	ITS accession	*trn*L-*trn*F accession	*mat*K accession
Olgaea pectinata Iljin	Kazakhstan, *Susanna 2187 et al.* (BC)	**AY826305**	**AY772343**	**AY785108**
Oligochaeta divaricata (Fisch. & C. A. Mey.) K. Koch	Garcia-Jacas et al., 2001	**AY826306**	**AY772344**	
Oligochaeta minima (Boiss.) Briq.	Uzbekistan, Tashkent Bot. Gard. (BC)	**AY826307**	**AY772345**	
Onopordum leptolepis DC.	Garcia-Jacas et al., 2002	AF319086, AF319140	—	AY013547
Onopordum nervosum Boiss.	France, Dijon Bot. Gard. (BC)	**AY826308**	**AY772346**	**AY785109**
Onopordum tauricum Willd.	Germany, Berlin Bot. Gard. (BC)	**AY826309**	**AY772347**	**AY785110**
Phonus arborescens (L.) G. López	Vilatersana et al., 2000 [as *Carthamus arborescens*]	AF140444, AF140445	—	—
Phonus riphaeus (Font Quer & Pau) G. López	Vilatersana et al., 2000 [as *Carthamus riphaeus*]	**AY826310**	**AY772348**	AY013512
Picnomon acarna (L.) Cass.	Garcia-Jacas et al., 2002	**AY826311**	**AY772349**	AY013549
Plagiobasis centauroides Schrenk	Kazakhstan, *Susanna 2130 et al.* (BC)	**AY826312**		
Polytaxis lehmanii Bunge	Tadjikistan, *Kamelin et al.* 23.4.86 (LE)	**AY826313**	**AY772350**	—
Polytaxis winkleri Iljin	Tadjikistan, *Botschantzev et al.* 27.4.82 (LE)	**AY826314**	—	—
Psephellus dealbatus (Willd.) K. Koch	Susanna et al., 1995 [as *Centaurea dealbata*]	L35886		
Psephellus gilanicus (Bornm.) Wagenitz	Garcia-Jacas et al., 2001 [as *Centaurea gilanica*]	**AY826315**	**AY772351**	AY013501
Psephellus incanescens (DC.) Boiss.	Garcia-Jacas et al., 2001 [as *Centaurea incanescens*]	AY012283, AY012319		
Psephellus persicus (DC.) Wagenitz	Garcia-Jacas et al., 2001 [as *Centaurea gaubae*]	**AY826316**	**AY772352**	AY013500
Psephellus pulcherrimus (Willd.) Wagenitz	Garcia-Jacas et al., 2001 [as *Aetheopappus pulcherrimus*]	**AY826317**	**AY772353**	AY013491
Psephellus xantocephalus (DC.) Fisch. & C. A. Mey.	Garcia-Jacas et al., 2001 [as *Centaurea xantocephala*]	**AY829445**		
Ptilostemon afer (Jacq.) Greuter	Garcia-Jacas et al., 2002	**AY826318**	**AY772354**	**AY785111**
Ptilostemon diacantha (Labill.) Greuter	Turkey, *Susanna 2313 et al.* (BC)	**AY826319**	**AY772355**	**AY785112**
Ptilostemon echinocephalus (Willd.) Greuter	Ukraine, *Romo 10365 et al.* (BC)	**AY829442**		
Ptilostemon hispanicus (Lam.) Greuter	Spain, *Mateos & García-García*, 18.9.98 (BC).	**AY829444**		
Rhaponticoides africana (Lam.) M. V. Agab. & Greuter	Susanna et al., 1995	L35863		
Rhaponticoides hajastana (Tzvel.) M. V. Agab. & Greuter	Garcia-Jacas et al., 2001	**AY826235**	**AY772279**	AY013502
Rhaponticum acaule DC.	Susanna et al., 1995	**AY826334**	**AY772369**	AY013515
Rhaponticum australe (Gaud.) Soskov	Australia, *Funk s.n.* (BC)	**AY826335**	**AY772370**	**AY785120**
Russowia sogdiana (Bunge) B. Fedtsch.	Tadjikistan, *Botschantzev* 5.5.75 (LE)	**AY826320**	—	—
Saussurea alpina (L.) DC.	Garcia-Jacas et al., 2002	AF319091, AF319145		
Saussurea asbukinii Iljin [=*Froloria asbukinii* (Iljin) Lipsch.]	Tadjikistan, *Kamelin* 24.6.70 (LE)	**AY826321**	**AY772356**	

Table 2. Continued.

Species	Voucher	ITS accession	*trn*L-*trn*F accession	*mat*K accession
Saussurea carduicephala (Iljin) Iljin [=*Lipschitziella carduicephala* (Iljin) Kamelin]	Tadjikistan, *Smakov & Dengubianko* 6.8.86 (LE)	**AY826322**	**AY772357**	—
Saussurea ceratocarpa Decne. [=*Lipschitziella ceratocarpa* (Decne.) Kamelin]	Raab-Straube, 2003	AJ606170, AJ606210	AJ606138	—
Saussurea deltoidea (DC.) Sch. Bip. [=*Himalaiella deltoidea* (DC.) Raab-Straube]	Raab-Straube, 2003	AJ606169, AJ606209	AJ606137	—
Saussurea discolor (Willd.) DC.	Garcia-Jacas et al., 2002	AF319092, AF319146	—	—
Saussurea elegans Ledeb.	Susanna et al., 2003	**AY826323**	**AY772358**	—
Saussurea frolowii Ledeb. [=*Frolovia frolowii* (Ledeb.) Raab-Straube]	Raab-Straube, 2003	AJ606171, AJ606211	—	—
Saussurea maximowiczii Herder	Susanna et al., 2003	**AY826324**	**AY772359**	—
Schischkinia albispina (Bunge) Iljin	Garcia-Jacas et al., 2001	**AY826325**	**AY772360**	**AY785113**
Schmalhausenia nidulans (Regel) Petr.	Susanna et al., 2003	**AY826326**	**AY772361**	AY373681
Serratula coronata L.	Garcia-Jacas et al., 2002	**AY826327**	**AY772362**	**AY785114**
Siebera pungens (Lam.) DC.	Turkey, *Susanna 2316 et al.* (BC)	**AY826328**	**AY772363**	**AY785115**
Silybum marianum (L.) Gaertner	Garcia-Jacas et al., 2002	**AY826329**	**AY772364**	AY013551
Staehelina baetica DC.	Garcia-Jacas et al., 2002	AF319095, AF319149	—	
Staehelina dubia L.	France, *Garnatje 25 & Luque* (BC)	**AY826330**	**AY772365**	**AY785116**
Staehelina fruticosa L.	Greece, Kriti, *Garnatje 147 & Luque* (BC)	**AY826331**	**AY772366**	**AY785117**
Staehelina lobelii DC.	Turkey, *Susanna et al. 2272* (BC)	**AY826332**	**AY772367**	**AY785118**
Staehelina uniflosculosa Sibth. & Sm.	Greece, *Raus & Royl 5479*, Berlin Bot. Gard. (BC)	**AY826333**	**AY772368**	**AY785119**
Stizolophus balsamita (Lam.) Cass. ex Takht.	Garcia-Jacas et al., 2001	**AY826336**	**AY772371**	**AY785121**
Stizolophus coronopifolius Cass.	Garcia-Jacas et al., 2001	**AY826337**	**AY772372**	AY013516
Synurus palmatopinnatifidus (Makino) Kitam.	Garcia-Jacas et al., 2002	**AY826338**	**AY772373**	AY013552
Syreitschikovia spinulosa (Franch.) Pavlov	Kazakhstan, *Susanna 2200 et al.* (BC)	**AY826339**	**AY772374**	**AY785122**
Tarchonanthus camphoratus L.	South Africa, *Ortiz* 17.3.02 (NBG)	**AY826340**	**AY772375**	**AY785123**
Tricholepis tibetica Hook. f. & Thomson	Pakistan, *Nüsser 1055* (B)	**AY826341**	—	—
Tugarinovia mongolica Iljin	Mongolia, *Trubov et al.* 1.7.89 (LE)	**AY826342**	**AY772377**	**AY785124**
Tyrimnus leucographus (L.) Cass.	Garcia-Jacas et al., 2002	**AY826343**	**AY772378**	AY013554
Volutaria crupinoides (Desf.) Maire	Garcia-Jacas et al., 2001	**AY826344**	**AY772379**	**AY785125**
Xeranthemum annuum L.	Turkey, *Susanna 2362 et al.* (BC)	**AY826345**	**AY772380**	**AY785126**
Xeranthemum cylindraceum Sm.	Denmark, Copenhagen Bot. Gard. (BC)	**AY826346**	—	—
Xeranthemum inapertum (L.) Miller	Garcia-Jacas et al., 2002	**AY826347**	**AY772381**	AY013555
Xeranthemum longepapposum Fisch. & C. A. Mey.	Kazakhstan, *Susanna 2182 et al.* (BC)	**AY826348**	**AY772382**	**AY785127**

Table 2. Continued.

Species	Voucher	ITS accession	*trn*L-*trn*F accession	*mat*K accession
Zoegea baldschuanica C. Winkl.	Uzbekistan, *Khassanov s.n.* (BC)	AY012305, AY012341	—	—
Zoegea leptaurea L.	Garcia-Jacas et al., 2000 [as *Z. mianensis*]	**AY826349**	**AY772383**	AY013517

added, and 40 cycles of 45 sec. denaturation at 94°C, 1 min. annealing at 58°C, 2 min. extension at 72°C, and a final 10 min. extension at 72°C. PCR products were cleaned with QIAquick PCR Purification Kit (Qiagen Inc., Valencia, CA) and sequenced with *trn*K-710 F and AST-1R primers. Direct sequencing of the amplified DNA segments was performed as for the *trn*L-*trn*F region.

*nr*DNA ITS REGION STRATEGIES

The three nuclear ITS1 spacer, 5.8 S gene, and ITS2 spacer (the ITS region) were amplified and sequenced together. The ITS region was amplified by PCR with 1406 F (Nickrent et al., 1994) and ITS1 (White et al., 1990) as forward primers, and ITS4 (White et al., 1990) as reverse primer, referring to the protocol described in Soltis and Kuzoff (1993). PCR products were purified using the QIAquick PCR Purification Kit (Qiagen Inc., Valencia, CA). Sequencing primers 1406 F and ITS4 were used. Direct sequencing of the amplified DNA segments was performed as for the *trn*L-*trn*F region.

PHYLOGENETIC ANALYSIS

Nucleotide sequences were edited with Chromas 1.56 (Technelysium, Tewantin, Australia). The *trn*L-*trn*F and *mat*K sequences were aligned visually by sequential pairwise comparison (Swofford & Olsen, 1990). The *mat*K sequences were translated for their putative proteins with GeneJockey (Biosoft, Cambridge, U.K.) to verify the absence of internal stop codons among those for amino acid codons. Due to the high level of variability of the ITS sequences, our alignment was checked with the ITS alignment for the whole Compositae by Goertzen et al. (2003) and adjusted manually. In order to conserve the phylogenetic information of insertions and deletions that constituted most of the variation of the *trn*L-*trn*F region, and at the same time avoid an overestimation of lengthy indels, they were coded as presence-absence characters and added to the end of matrices in the combined analyses. The aligned data matrices are available on request from the corresponding author.

The ITS matrix was analyzed by Bayesian inference, because heuristic parsimony search was impossible due to the size of the data matrix (190 species; the search for most-parsimonious trees was too time-consuming and soon became unpractical). Bayesian inference (BI) estimation was calculated using MrBayes 3.01 (Ronquist & Huelsenbeck, 2003). The best-available model of molecular evolution, required for Bayesian estimations of phylogeny, was selected using hierarchical likelihood ratio tests (hLRT) and Akaike information criteria (AIC) as implemented in the software MrModeltest 1.1b (Nylander, 2002), which considers only nucleotide substitution models that are currently implemented in PAUP and MrBayes 3.01 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The best-fit model of nucleotide substitution for the ITS dataset was the same in both methods: the symmetrical model, with some sites assumed to be invariable and variable sites assumed to follow a discrete gamma distribution (GTR+I+G; Yang, 1996). Bayesian inference analyses were initiated with random starting trees and were run for 1×10^6 generations. Four Metropolis-coupled Markov chain Monte Carlo (MCMC) chains were sampled every 100 generations, which resulted in 10,000 sample trees. A critical aspect of the Bayesian analysis is to ensure that the Markov chain has reached stationarity. All sample points prior to stationarity are essentially random and are discarded as "burn-in" 1,000 samples trees, because they do not contain useful parameter estimates. Internodes with posterior probabilities $\geq$ 95% were considered statistically significant. A majority-rule consensus tree was calculated with PAUP version 4.0b4a (Swofford, 1999). Posterior probability support (PP) was estimated to be significant for nodes with PP $>$ 0.95.

For the combined data sets, parsimony analysis involved heuristic searches conducted with PAUP version 4.0b10 (Swofford, 1999) using Tree Bisection Recognition (TBR) branch swapping with character states specified as unordered and unweighted. All most parsimonious trees (MPT) were saved. To locate islands of most parsimonious trees (Maddison, 1991), we performed 100 replicates with random taxon addition, and with TBR branch swapping. Tree lengths, consistency index (CI), and retention index

Table 3. Comparison of results from the ITS, ITS + *trn*L-*trn*F, and ITS + *trn*L-*trn*F + *mat*K data sets. The consistency and homoplasy indices are calculated by excluding uninformative characters.

Data set	ITS	ITS + *trn*L-*trn*F	ITS + *trn*L-*trn*F + *mat*K
Number of taxa	190	121	111
Total characters	519	1699	2708
Informative characters	390	493	677
Number of MPTs	—	298	3122
Number of steps	—	2970	3288
Islands	—	8	5
Consistency index (CI)	—	0.2914	0.3259
Retention index (RI)	—	0.6800	0.6783
Homoplasy index (HI)	—	0.7086	0.6741
Range of divergence, ingroup (%)	0–5	0.13–2.43	0.12–1.8

(RI) are always given, excluding uninformative characters. Two combined analyses were performed, with different data sets: the ITS + *trn*L-*trn*F sequence data and the ITS + *trn*L-*trn*F + *mat*K data.

Bootstrap (BS) and Bremer support (Bremer, 1988; Donoghue et al., 1992) or decay index (DI) were carried out to obtain support estimates for the nodes in the consensus trees. Bootstrap analysis was performed (Felsenstein, 1985) using 1000 replicates and heuristic search with the default options. In the nrDNA ITS data matrix, we used the approach by Lidén et al. (1997) using 1000 replicates, random taxon addition with 20 replicates, and no branch swapping. For the two combined matrices, DI was calculated for each node by successive analyses using the clade constraint approach, as discussed in Morgan (1997), with 10 replicates. ACCTRAN (accelerated transformation) character-state optimization was used for all illustrated trees.

Results and Discussion

Since we were unable to obtain DNA sequences for all three genic regions for every taxon sampled, we performed three distinct analyses: (1) ITS alone, to examine the position of some genera not included in previous analyses and for which we were not able to amplify any chloroplast region; (2) ITS and *trn*L-*trn*F regions combined, to study the generic limits in the *Saussurea* group; and (3) the three regions (ITS, *trn*L-*trn*F, and *mat*K) combined, to elucidate subtribal limits and to confirm the naturalness of the informal groups in Carduinae. The numeric results of the three analyses are summarized in Table 3. The resulting trees are shown in Figure 1A and 1B (Bayesian majority rule consensus for the ITS dataset alone), Figure 2 (parsimony strict consensus of the combined ITS and *trn*L-*trn*F sequences), and Figure 3 (parsimony strict consensus of the combined ITS, *trn*L-*trn*F and *mat*K sequences). The Bayesian majority rule consensus trees of the two combined data sets are largely coincident with the parsimony consensus trees, and therefore we have added the Bayesian support (PP) to those branches that have PP > 0.95 but are not, or are only weakly, supported by parsimony (Figs. 2, 3). Only the Carlininae branch in the combined Bayesian analysis of the three regions is illustrated (Fig. 4), because it confirms the position of *Tugarinovia* within Carlininae.

Delineation of Cardueae

The monophyly of Cardueae was confirmed with the new outgroup in all the analyses with high statistical support: PP = 1.00 (Fig. 1A), BS = 100%, 100% (Figs. 2, 3), and DI = 11 (Figs. 2, 3). Thus, the most appropriate status for Echinopinae and Carlininae is subtribal. Indeed, Cardueae could be divided into five tribes, but we consider it unpractical to fragment a natural group that can be so easily recognized on the basis of macromorphology.

Subtribal Classification

The four subtribes recognized by the latest report on the tribe (Garcia-Jacas et al., 2002), Carlininae, Echinopinae, Carduinae, and Centaureinae, were confirmed. Subtribe Cardopatiinae must be restored and some changes made to correlate molecular phylogeny and subtribal delineation. However, in view of the moderate support for these basal branches (they collapse in a polytomy in all the Bayesian analyses, cf. Fig. 1A), subtribes Carlininae, Echinopinae, and Cardopatiinae should be considered a currently unresolved polytomy basal to Carduinae–Centaureinae.

Carlininae and *Tugarinovia*

Our results do not modify the circumscription of Carlininae in our latest surveys of Cardueae (Garcia-

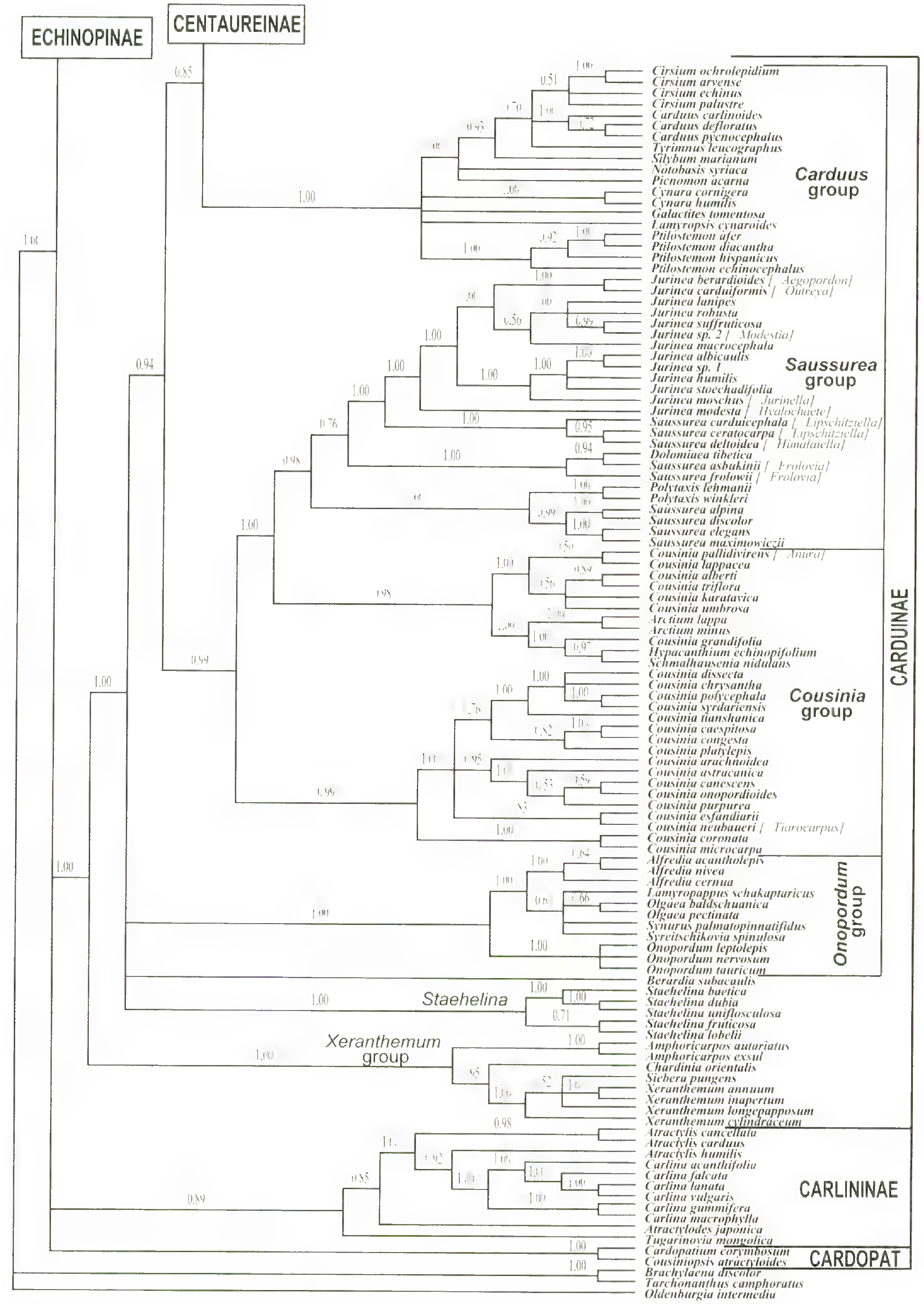

Figure 1. (pp. 162–163). —A (p. 162). Bayesian majority rule consensus tree of the ITS sequence data matrix (basal part of the tree only). Numbers above branches are Bayesian Posterior Probabilities (PP). CARDOPAT = Cardopatiinae. —B (p. 163). Bayesian majority rule consensus tree of the ITS sequence data matrix (upper part of the tree only). Numbers above branches are Bayesian Posterior Probabilities (PP).

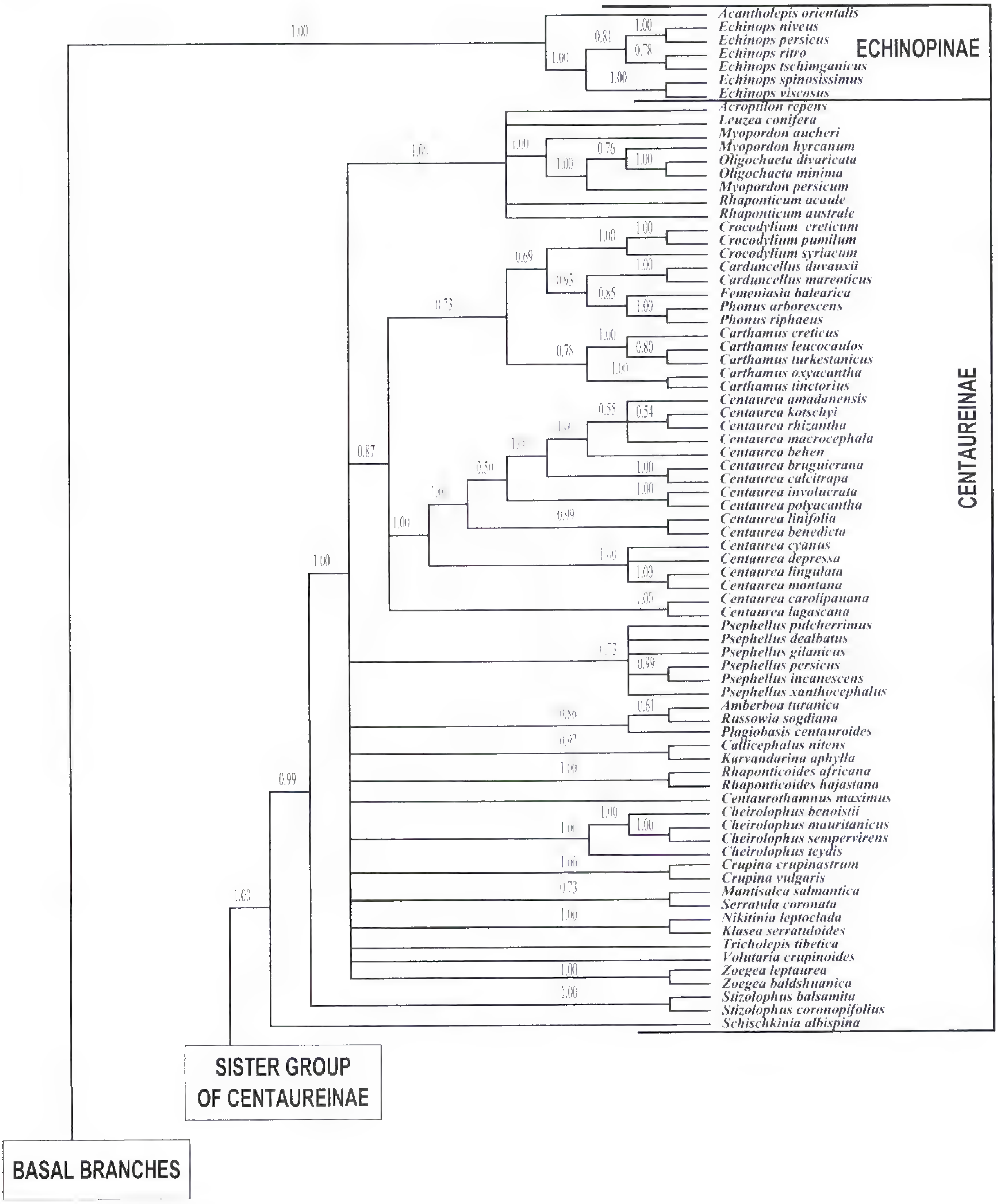

Figure 1. Continued.

Jacas et al., 2002; Susanna & Garcia-Jacas, in press). The subtribe is monophyletic without Bayesian support in the ITS analysis (PP = 0.89, Fig. 1A) and with high support in the combined analyses (BS = 95%, DI = 7, Fig. 2; BS = 100%, DI = 9, Fig. 3), and includes *Atractylodes* DC., *Atractylis*, *Carlina* L., and *Thevenotia* DC. (not included in present analyses, but confirmed in our previous work). The remaining genera that were classified by other authors (Dittrich, 1977, 1996b; Bremer, 1994) in Carlininae belong either to Carduinae (*Staehelina* and the *Xeranthemum* group) or Cardopatiinae (*Cardopatium* and *Cousiniopsis*), based on molecular phylogenies as suggested by the sequence data. The classic definition of Carlininae was based mainly on achene characters (Dittrich, 1977, 1996b): parenchymatic pericarp usually hir-

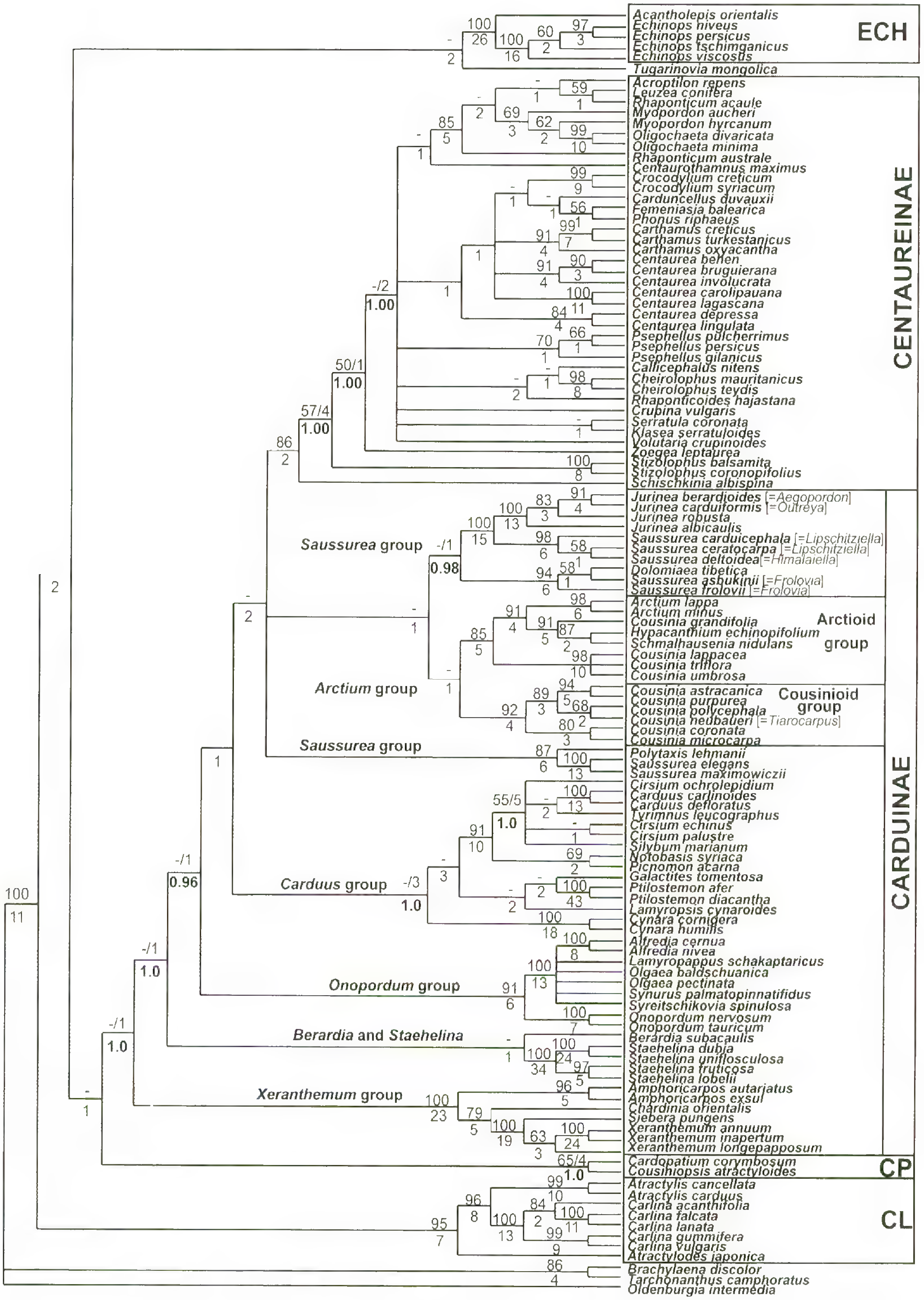

Figure 2. Strict consensus tree of the most parsimonious trees resulting from the ITS and *trn*L-*trn*F combined data matrix. Bolded numbers are Bayesian Posterior Probabilities (PP) which are detailed only for branches unsupported by parsimony bootstrap. Numbers above branches or before a slash are bootstrap percentages (BS); below branches or after a slash, decay indices (DI). A dash indicates bootstrap support less than 50%. Abbreviations of subtribes: CL = Carlininae; CP = Cardopatiinae; ECH = Echinopinae.

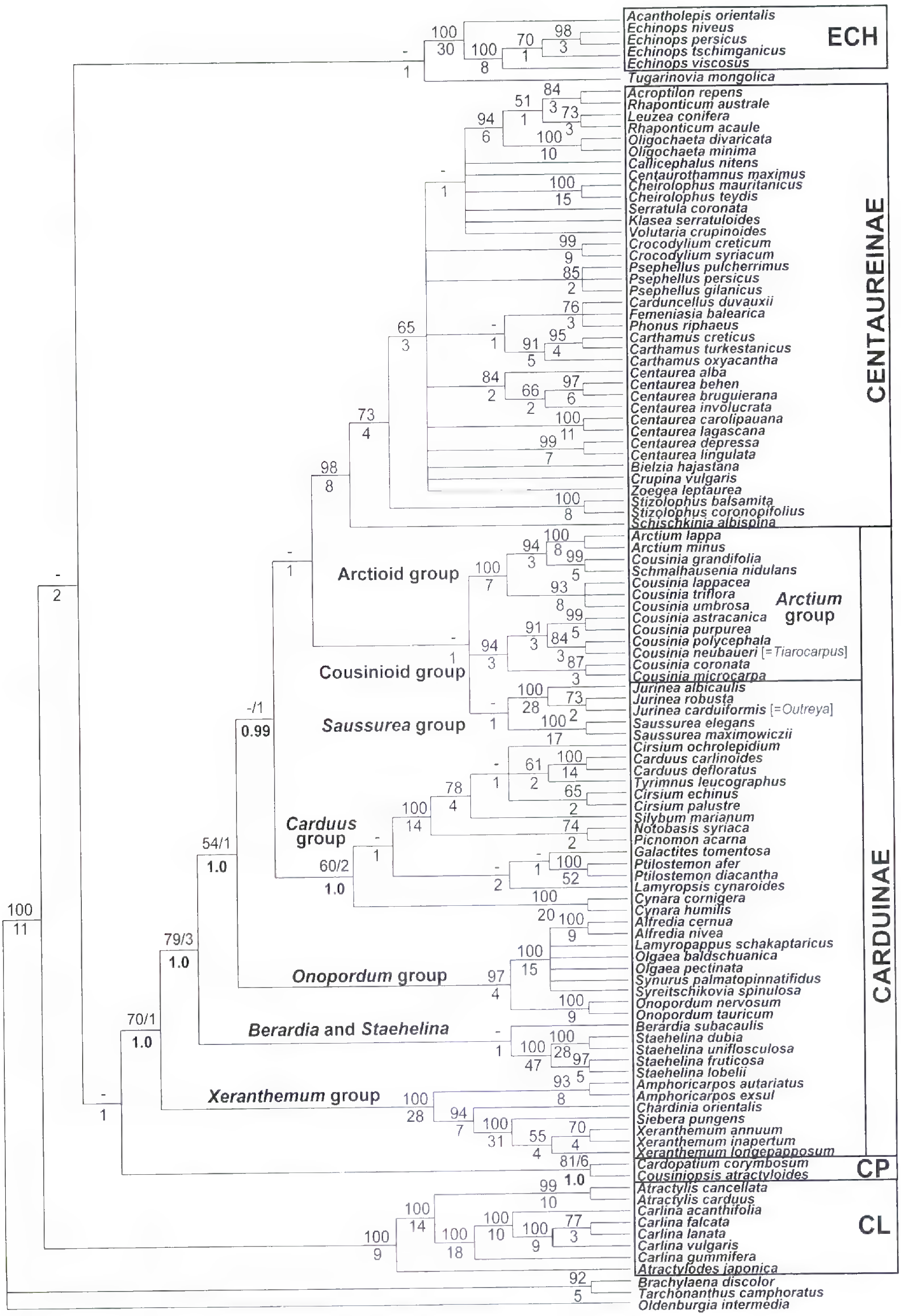

Figure 3. Strict consensus tree of the most parsimonious trees resulting from the ITS, *trn*L-*trn*F, and *mat*K combined data matrix. Bolded numbers are Bayesian Posterior Probabilities (PP) detailed only for branches unsupported by parsimony bootstrap. Numbers above branches or before a slash are bootstrap percentages (BS); below branches or after a slash, decay indices (DI). A dash indicates bootstrap support less than 50%. Abbreviations of subtribes: CL = Carlininae; CP = Cardopatiinae; ECH = Echinopinae.

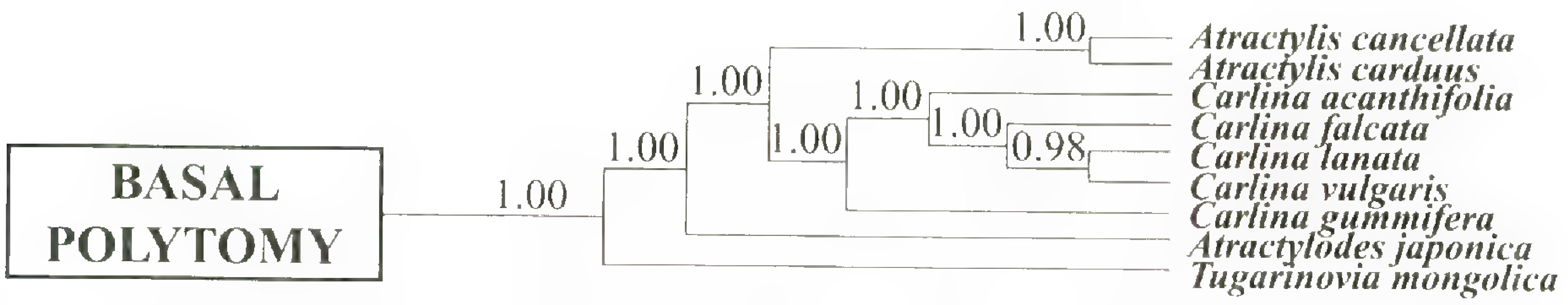

Figure 4. Detail of the branch of the subtribe Carlininae from the Bayesian majority rule consensus of the ITS, *trn*L-*trn*F, and *mat*K combined data matrix. Numbers above branches are Bayesian Posterior Probabilities (PP).

sute, and pappus setae very long with plumose directly attached to the pericarp. However, these characters must be interpreted as plesiomorphic, because they appear across all basal subtribes (Carlininae, Cardopatiinae, and Echinopinae) and even in Carduinae. If we rely only on achene characters for classification, the resulting definition of Carlininae (Dittrich, 1977, 1996b) differs greatly from the delineation on the basis of DNA sequence analyses and macromorphology (Susanna & Garcia-Jacas, in press).

Our molecular analyses confirm that *Tugarinovia*, a puzzling monotypic genus of dioecious plants from Mongolia that was placed in Carlininae by Dittrich et al. (1987), belongs to Cardueae. Curiously, this subtribal placement is supported only by the Bayesian combined analysis of the three regions (PP = 1.0, Fig. 4). Indeed, the only subtribe where it can be placed on the basis of morphological affinities (leaves, involucral bracts, and pappus) is Carlininae (Dittrich et al., 1987; Susanna & Garcia-Jacas, in press). Our analyses show no connection of *Tugarinovia* with the only other East Asian representative of Carlininae, *Atractylodes*, or with any other genus of the subtribe, reinforcing its isolated position.

Cardopatiinae

This subtribe had moderate support in our parsimony analyses (BS = 65%, 81%; DI = 4, 6; Figs. 2, 3), perhaps due to the different evolutionary rates of annual *Cousiniopsis* and perennial *Cardopatium*. The Bayesian support for this branch, however, is very high (PP = 1.00, Figs. 1A, 3, 4).

Subtribe Cardopatiinae, as first defined, included only the east Mediterranean genus *Cardopatium*. Later, Nevski (1937) described a monotypic genus from central Asia, *Cousiniopsis*, closely related to *Cardopatium* (it was first described as *Cardopatium atractyloides* C. Winkler). Classic monographers of Compositae (Bentham, 1873; Hoffmann, 1894; Dittrich, 1977; Bremer, 1994) consistently placed both genera among Carlininae, but the only characters that connect these two groups are those of achenes, which could equally relate *Cardopatium* and *Cousiniopsis* to Echinopinae. It is tempting to interpret the corymbose inflorescence of *Cardopatium*, formed by very small, few-flowered capitula, as a first step towards syncephaly. On this basis, Petit (1997) considered *Cardopatium* sister to *Echinops* L. and placed *Cardopatium* and *Cousiniopsis* in Echinopinae. On the basis of our results, we prefer to interpret these similarities as convergence, because syncephalies at various states of development involving small, few-flowered heads occur in all the subtribes across Cardueae (Garcia-Jacas et al., 2002).

Echinopinae

Our results demonstrate, contrary to our previous studies (Garcia-Jacas et al., 2002), that Echinopinae include only *Echinops* s.l. (*Echinops* and *Acantholepis* Less.) with strong support (PP = 1.00, Fig. 1B; BS = 100%, DI = 26, 30, Figs. 2, 3). In fact, a recent molecular study indicates that *Acantholepis* is a reduced, unarmed species of *Echinops* (Garnatje et al., 2005), as originally described (*Echinops acantholepis* Jaub. & Spach). Our combined analyses reveal that the *Xeranthemum* group does not belong to Echinopinae, but rather to Carduinae as sister to the rest of this subtribe (Figs. 1A, 2, 3).

The origin of the compound inflorescence of *Echinops* cannot be tracked on molecular grounds, because the subtribe does not show supported affinity to any other group in Cardueae. Cardopatiinae and Carlininae are the best candidates for sister groups to the subtribe Echinopinae (because the structure of the achenes is very similar, cf. Dittrich, 1977).

Carduinae

If monophyletic Centaureinae are recognized as a distinct subtribe, the Carduinae constitute a paraphyletic assemblage (Figs. 1A, 2, 3). However, alternate solutions are not practical. Either a subtribe level is ascribed to all the monophyletic groups recognized in present Carduinae and a fragmented classification results, or a single large subtribe Carduinae, including Centaureinae, is maintained,

which thereby encompasses almost ninety per cent of the species of the tribe (Garcia-Jacas et al., 2002).

Even in this disparate assemblage, some well-defined groups emerge, together with genera without known affinities like *Berardia* or *Staehelina*.

BERARDIA AND *STAEHELINA*

Our molecular analyses show that these two genera present no obvious affinities. They cluster in an isolated position within Carduinae, in both combined analyses, without statistical support (Figs. 2, 3). *Berardia* was ranked among Mutisieae on the basis of achene characters (Dittrich, 1977) and we agree in that the pericarp cells, with thickened u-shaped walls, are very similar to the type found in Gochnatiinae Benth. & Hook. f., a subtribe of Mutiseae (Dittrich, 1996a). Further support for the, albeit weak, relationship between *Berardia* and *Staehelina* is that the pericarp of *Staehelina* is also "gochnatioid" (Dittrich, 1996a). However, we cannot state whether this similarity represents convergence or is a very old character conserved in these two anomalous genera.

Staehelina was previously placed among Carlininae (Bentham, 1873; Hoffmann, 1894; Dittrich, 1977; Bremer, 1994), but Petit (1997) proposed moving it to Carduinae. For Dittrich (1996b), the two species of *Staehelina* with hirsute pericarp (*S. fruticosa* L. and *S. lobelii* DC.) should be classified in a distinct genus, *Hirtellina* Cass. All our analyses grouped the included species of *Staehelina* (five out of eight) in a robust clade with very high support (PP = 1.00, Fig. 1A; BS = 100%, DI = 34, 47, Figs. 2, 3). However, both combined analyses divided the genus into two well-supported clades that coincide with *Staehelina* s.s. and *Hirtellina* (Figs. 2, 3), which is compatible with the division of the genus. Nevertheless, morphological differences other than presence or absence of achene pilosity are virtually non-existent, and we prefer to keep a single genus with *Staehelina* and *Hirtellina* recognized at sectional rank within *Staehelina* (Susanna & Garcia-Jacas, in press).

THE *XERANTHEMUM* GROUP

In a previous study, the *Xeranthemum* group (genera *Amphoricarpos*, *Chardinia* Desf., *Siebera*, and *Xeranthemum*) was placed among subtribe Echinopinae. This unexpected result led us to propose that the very small and peculiar heads of the genera of the group, with very large receptacular bracts, could constitute a syncephaly (Garcia-Jacas et al., 2002). Our new analyses show that this view was erroneous and, in fact, Harris (1995) had already demonstrated that the inflorescence of *Xeranthemum* was not a syncephaly. Indeed, the *Xeranthemum* group appears, in the combined analyses, as part of the Carduinae, sister to the rest of the subtribe, with low parsimony bootstrap support but very high Bayesian support (PP = 1.00, Figs. 1A, 2, 3), in an isolated position. The monophyly of the group also has very high support (PP= 1.00, Fig. 1A; BS = 100%, DI = 23, 28, Figs. 2, 3). Traditional classification (Dittrich, 1977; Bremer, 1994) placed it in Carlininae, and Petit (1997) was the first to suggest Carduinae. Species of three of the genera of the group (*Chardinia*, *Siebera*, and *Xeranthemum*) are annual colonizers of arid and waste-land thoroughout the Mediterranean region. In contrast, species of the dwarf shrubby genus *Amphoricarpos* are narrow mountain endemics, sister to the rest of the genera of the *Xeranthemum* group in all the analyses (Figs. 1A, 2, 3).

THE *ONOPORDUM* GROUP

The usual definition of this group is based on the absence of receptacular bracts. A pitted, naked receptacle is otherwise rare in the tribe. However, not all the species of at least one genus (*Alfredia* Cass.) show an epaleate receptacle. In addition to this character, achenes are also peculiar with pericarp diversely pitted, wrinkled, or rugulose (Susanna & Garcia-Jacas, in press), but seldom smooth (*Olgaea* and *Syreitschikovia*). The group has considerable negative importance, because species of *Onopordum* include some highly noxious weeds widespread in the Mediterranean region and the American west like *O. acanthium* L. and *O. nervosum* Boiss., giant thistles that can reach up to 3 m high.

Three genera not included in previous studies, *Lamyropappus*, *Olgaea*, and *Syreitschikovia*, are classified in the *Onopordum* clade in all three analyses, which confirm the group as a natural one with significant support (PP = 1.00, Fig. 1A; BS = 91%, 97%, DI = 6, 4, Figs. 2, 3). *Syreitschikovia* had been previously placed by Dittrich (1977) and Bremer (1994) in Centaureinae. Its classification in Carduinae and its relationship to the *Onopordum* group was reported by Susanna et al. (2002) on the basis of morphology.

Generic definitions in the group are unclear, with the only exception of *Onopordum*. *Alfredia* forms a polytomy with *Lamyropappus*, *Olgaea*, *Synurus* Iljin, and *Syreitschikovia* (Figs. 1A, 2, 3). The inclusion of more species of *Olgaea*, which comprises some 15 taxa from the Tien Shan mountains of Kyrgyzstan and Tajikistan, and its strange relative *Takeikadzuchia* Kitag. & Kitam. from Mongolia, may contribute to a better definition of the genera in the group.

THE *CARDUUS* GROUP

This represents a large complex of very spiny plants which are usually called thistles. All share medium or large-sized heads, spiny leaves, and a long pappus detachable as a single piece. Our results indicate that a large number of the genera (*Carduus* L., *Cirsium* Mill., *Notobasis* Cass., *Picnomon* Adans., *Silybum* Adans., and *Tyrimnus* Cass.) form a natural group with significant parsimony support (BS = 91%, 100%, DI = 10, 14, Figs. 2, 3). Remaining genera, *Cynara* L., *Galactites* Moench, *Lamyropsis* (Kharadze) Dittrich, and *Ptilostemon* Cass., are also placed in this group in all analyses, but this is only supported by the Bayesian analyses (PP = 1.00 in all the cases, Figs. 1A, 2, 3).

As pointed out by Häffner and Hellwig (1999) and Garcia-Jacas et al. (2002), phylogenetic relationships and generic boundaries within the clade are obscure (Fig. 1A, 2, 3). One of the reasons for this is that the co-existence of annual or biennial species (most of *Carduus*, *Galactites*, *Picnomon*, *Silybum*, or *Tyrimnus*) together with perennials (many *Cirsium*, *Cynara*, *Lamyropsis*, and *Ptilostemon*) hinders the assessment of the two aspects from a molecular standpoint. Differences in mutation rates between annuals and perennials (Gaut et al., 1997; Laroche et al., 1997; Andreasen & Baldwin, 2001) make comparison of DNA sequences a less reliable tool. In fact, unexpected results, like the strange position of the annual genus *Galactites*, could be a result of these differences; *Galactites* is placed close to the base of the thistles in the combined analyses, grouped with *Ptilostemon* (Figs. 2, 3), thereby contradicting morphological evidence (*Galactites* is morphologically similar to *Carduus* or *Cirsium*). *Lamyropsis*, the only genus of the thistles missing in our previous studies and sequenced here for the first time, appears related to *Ptilostemon* in the combined analyses, without support (Figs. 2, 3). Species of *Lamyropsis* have dentate-spiny leaves with very prominent veins beneath, similar to many species of *Ptilostemon*. The affinities between the two genera were pointed out by Dittrich (1971).

Taking into account our low sampling for such an enormous group (ca. 500 species in total), any concluding remark on the thistles would be premature. The *Carduus* group, together with the two following ones, requires a more comprehensive molecular analysis.

THE *ARCTIUM* GROUP

This group has been the subject of a recent preliminary molecular survey, using ITS and *matK* sequences (Susanna et al., 2003). The results herein, including the *trnL-trnF* region (Figs. 2, 3), do not change our previous main conclusions that the limits of *Arctium* L. and *Cousinia* are unclear. Our study (Susanna et al., 2003) demonstrated two principal clades in the *Arctium* group: the Arctioid clade (supported only by the two combined analyses with BS = 85%, 100%, DI = 5, 7, Figs. 2, 3) and the Cousinioid clade (supported by all three analyses with PP = 0.99, Fig. 1A.; BS = 92%, 94%, DI = 4, 3, Figs. 2, 3). The two groups can be segregated by molecular, chromosome, and pollen characters, but this grouping is not consistent with morphology: two genera of the group, *Schmalhausenia* C. Winkl. and *Hypacanthium* Juz., are affined with *Arctium* on the basis of pollen, chromosomes, and DNA sequences (Figs. 1A, 2), but in other respects are morphologically much closer to *Cousinia*. In addition to an Arctioid species group within *Cousinia*, there is also a Cousinioid group seen in *Arctium*. More sampling of the obscure *Cousinia* subgenus *Hypacanthodes* Tscherneva from Central Asia is required, but it is highly probable that all four genera will have to be grouped in *Arctium*.

Finally, our ITS analysis (Fig. 1A) confirms that the purported genera *Anura* and *Tiarocarpus*, as previously proposed by Susanna and Garcia-Jacas (in press), cannot be segregated from *Cousinia*, to which they are united with good support (PP = 1.00 in both cases, Fig. 1A).

THE *SAUSSUREA* GROUP

The only genera placed in the *Saussurea* group by Susanna and Garcia-Jacas (in press) that were not included in our previous studies are *Dolomiaea* and *Polytaxis*. The ITS and the combined ITS + *trnL-trnF* analyses place *Polytaxis* basal to *Saussurea* with high Bayesian (PP = 0.99, Fig. 1A; PP = 1.00, Fig. 2) and good parsimony support (BS = 87%, DI = 6, Fig. 2). Because species of *Polytaxis* are the only annual taxa in this clade, its basal position could originate in the faster evolution of annuals relative to perennials (Gaut et al., 1997; Laroche et al., 1997; Andreasen & Baldwin, 2001), in the same way that annual *Acantholepis* always appears basal to perennial *Echinops* (Fig. 1B, 2, 3). By its side, *Dolomiaea* is grouped with high support (PP = 1.00, Fig. 1A; BS = 94%, DI = 6, Fig. 2) in the ITS and the combined ITS and *trnL-trnF* analyses with *Frolovia* (*Saussurea asbukinii* Iljin and *S. frolovii* Ledeb.). It seems adequate to consider *Frolovia*, a genus restored by Raab-Straube (2003), a synonym of *Dolomiaea*.

Another taxon that was not included in our previous study is the purported genus *Aegopordon* (*Jurinea*

berardioides (Boiss.) O. Hoffm. in Figs. 1A, 2), which, according to Susanna and Garcia-Jacas (in press), should be considered a synonym of *Jurinea*. The combined ITS + *trn*L-*trn*F analysis (Fig. 2) place it in a robust clade (BS = 91%, DI = 4) with *Jurinea carduiformis* (Jaub. & Spach) Boiss., formerly also considered a distinct genus (*Outreya* Jaub. & Spach) that we merged in *Jurinea* (Garcia-Jacas et al., 2002).

Our results confirm that the limits between *Jurinea* and *Saussurea* are not well established (as pointed out recently by Kita et al., 2004), because some species formerly included in *Saussurea* are grouped in the genus *Jurinea* (Figs. 1A, 2). *Saussurea carduicephala* (Iljin) Iljin and *S. deltoidea* (DC.) Sch. Bip. were considered by Raab-Staube (2003) as the distinct genus *Himalaiella*. *Saussurea ceratocarpa* Decne. was for Raab-Staube (2003) a restored genus *Lipschitziella*. Both purported genera form a robust clade in the ITS and the ITS + *trn*L-*trn*F analysis (PP = 1.00, Fig. 1A; BS = 98%, DI = 6, Fig. 2). According to this result, if we grant the genus level to this clade, *Himalaiella* should be considered a synonym of *Lipschitziella*. However, we prefer to consider it a synonym of *Jurinea*, because both purported *Himalaiella* and *Lipschitziella* form a monophyletic clade with *Jurinea* s. str., with very high support (PP = 1.00, Fig. 1A; BS = 100%, DI = 15, Fig. 2).

No final conclusions can be drawn from this entanglement of genera, because our sampling of *Jurinea* was very limited. However, a redefinition of the boundaries between *Jurinea* and *Saussurea* is clearly required. The clarification of these limits, and indeed the description of new genera in a complex in which no less than 15 have been already described (Susanna & Garcia-Jacas, in press), calls for a much more comprehensive sampling than any performed to date.

CENTAUREINAE

Our results confirm the general outline of Centaureinae proposed by Garcia-Jacas et al., 2001, this time on the basis of three regions of the genome (Figs. 1B, 2, 3). Here we describe only the most important results, namely the inclusion of two genera formerly classified in Carduinae, *Myopordon* and *Nikitinia*, in the subtribe.

Myopordon was considered related to *Onopordum* (hence the name) and placed in subtribe Carduinae because of the absence of receptacular setae (Wagenitz, 1958; Dittrich, 1977). In contrast, the ITS analysis relates *Myopordon* to the genus *Oligochaeta* K. Koch of subtribe Centaureinae with very high support (PP = 1.00, Fig. 1B), and the combined ITS + *trn*L-*trn*F analysis places *Myopordon* deeply nested in the *Rhaponticum* Vaill. group with high support (BS = 85%, DI = 5, Fig. 2). Difficulties in interpretation of, even apparently unambiguous, characters consistently occur in tribe Cardueae: as we have seen above, the naked receptacle is a supported character of the *Onopordum* group (Susanna & Garcia-Jacas, in press), but there are many exceptions. Epaleate genera are present in almost every subtribe: *Tugarinovia* in Carlininae, *Dolomiaea* and part of the *Onopordum* group in Carduinae, and *Myopordon* and *Russowia* C. Winkl. in Centaureinae. To verify the position of *Myopordon* within Centaureinae on morphological grounds, the characters of the achenes are critical; however, we were unable to find herbarium material with mature fruits. Mouterde (1983) described the insertion areole of the achenes as oblique, a character of Centaureinae. This observation contrasts with that of Wagenitz (1958), who reported the insertion as straight, which therefore points towards Carduinae.

Nikitinia was described in Carduinae, and in recent reviews of the tribe was maintained in that subtribe (Dittrich, 1977; Bremer, 1994). However, achene characters are undoubtedly centauroid (especially the double pappus, illustrated in Susanna et al., 2002) and relate it to the genus *Klasea* Cass. as confirmed by molecular analyses (PP = 1.00, Fig. 1B).

Concluding Remarks

With a more suitable outgroup and with the addition of the *trn*L-*trn*F region, the systematics of Cardueae now appears to be more fully resolved. However, there are taxonomic issues that remain unclear and their clarification requires better sampling and more morphological and molecular data. In addition to only moderate support for basal branches in the combined analysis of the three regions, doubts remain regarding problems typical of delimitation of very large genera such as are frequently found in Compositae (classic examples are *Aster* L., *Erigeron* L., or *Senecio* L.). In Cardueae, generic boundaries are difficult to establish for *Carduus*, *Cirsium*, *Cousinia*, *Jurinea*, and *Saussurea*. In the case of *Carduus* and *Cirsium*, extensive sampling in Africa and North America is needed. For *Cousinia*, *Jurinea*, and *Saussurea*, which are the easternmost representatives of the tribe in Eurasia, intensive collections are called for in Central and East Asia.

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LATIN AMERICAN BIOGEOGRAPHY—CAUSES AND EFFECTS. INTRODUCTION[1, 2, 3, 4]

Alan Graham[5]

The 51st Annual Systematics Symposium held at the Missouri Botanical Garden, October 8–10, 2004, had as its theme *Latin American Biogeography—Causes and Effects*. The papers in this volume were either presented at the symposium or are invited papers by specialists on related topics. The fall of 2004 was an appropriate time to consider patterns of plant and animal distributions within Latin America and their affinities with other lands because it was 30 years ago, in the fall of 1974, that Raven and Axelrod published their landmark paper, "Angiosperm biogeography and past continental movements," in the *Annals of the Missouri Botanical Garden*. That paper did much to revitalize interest in biogeography and to modernize prevailing views about the physical context within which these patterns and affinities originated. It still resonates well today because it focused attention on two components essential to understanding the arrangement of organisms and communities over the landscape. One is the need for a taxonomy that reflects distributions that are biologically meaningful rather than ones that are

[1] This and the 10 articles that follow it are the proceedings of the 51st Annual Systematics Symposium of the Missouri Botanical Garden, *Latin American Biogeography—Causes and Effects*. The symposium was held 8–10 October, 2004 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

[2] This was the 49th Missouri Botanical Garden Annual Systematics Symposium to be supported by a grant from the National Science Foundation (grant DEB-9981642). Among the many persons contributing to the planning and operation of the meeting and to the publication of the papers are Olga Martha Montiel (Center for Conservation and Sustainable Development); Mick Richardson (Research, Graduate Studies), Alina Freire-Fierro, and Sandy Lopez; Victoria Hollowell (Director, Missouri Botanical Garden Press), Carmen Ulloa Ulloa, Amy McPherson, and Beth Parada; Donna Miller and Zubin Chandran (Information Technology); William Guy (Facility Support); and Mary McNamara (registration). This symposium, together with 31 previous ones, again benefited considerably from the contributions, support, and encouragement of Peter Raven.

[3] This symposium volume is dedicated to Barbara W. Leyden, our esteemed colleague and an invited speaker to the Symposium, who died in February 2006. She established herself as an important contributor to Quaternary vegetation history and paleoecology through papers on rapid climate change and periods of aridity at glacial-interglacial boundaries in Guatemala and in the Lake Valencia Basin, Venezuela. Barbara gained further international reputation and respect for her later work on the environments of the Lowland Maya region of the Yucatán Peninsula and adjacent Central America. We join with our editor Victoria Hollowell in celebrating her critical and broad-based expertise and her vibrant contributions to the literature.

[4] The editors of the *Annals* thank Sophia Balcomb for her significant editorial contribution to these papers.

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artifacts of nomenclature. The other is the need for sound models of landscape evolution and environmental change as a context for reconstructing migrations through time.

An outgrowth of this revitalization in biogeography has been the application of new information and analysis from molecular biology (phylogeography) to augment and test long-standing knowledge derived from traditional approaches. There are now more accurate and temporally exact models of plate tectonics (Pindell, 1994; Pindell & Barrett, 1990; Mann, 1999), and there is a better appreciation of its consequences, including the direction and rates of crustal movement, the reconstruction of land bridges, the uplift of mountain systems and plateaus, and the partitioning of populations by changes in drainage systems. There is also an expanding paleontological basis for tracing the effects of these events on the distribution of lineages and communities and an increasing awareness of the impressive arsenal of techniques from independent disciplines now available for reconstructing environmental change and the biotic responses (see below).

Also important, but still in the formative stage, is development of a database of fossil plants that provides a more complete and reliable checklist of taxa and their age. Identifications of megafossils in the older literature are notoriously unreliable, as are many of the biological affinities cited in stratigraphic palynological publications for Cretaceous and Cenozoic plants. It is incomprehensible in this modern era that key information for fossil plant remains is so inaccessible. These data are badly needed for dating phylogenies, calibrating molecular clocks, and conducting studies on vicariance and dispersal. They are also valuable as historical background for formulating speciation models and in making paleoenvironmental reconstructions as analogues for the effects of current environmental trends. The online electronic framework for such databases already exists, but a coordinated effort by paleobotanists will be required to filter into the system more complete records assessed for accuracy.

The new analytical tools available, and the novel concepts being generated, are part of the reason for renewed interest in biogeography. There have been three major symposia devoted to the subject within the past three years—*Tropical Intercontinental Disjunctions*, organized by Susanne Renner and Thomas Givnish (2004); *Long-Distance Dispersal*, edited by Michael Cain, Ran Nathan, and Simon Levin (2003); and the present volume.

The goals herein are, first, to illustrate and update present and past distributions for several major groups of organisms, with particular reference to Latin America and other lands of the Southern Hemisphere. Second, to document some of the forcing mechanisms, especially plate tectonics, land bridges, and climatic change, that help explain former distributions and their residual patterns in the modern biota. Third, to show the variety of methodologies now available for documenting these forcing mechanisms and their biological consequences. The most enlightening of these methodologies often come from outside the biological sciences and include satellite imagery of atmospheric events; recent innovations in quick-time, detailed, multi-factored paleogeographic computer animations (Scotese, 2004); geochemistry; geophysics; marine sedimentology; and the myriad of factors determining weather and longer-term climate. Relationships between seemingly disparate observations are a rich source of new insights into biogeographic problems unresolved by traditional approaches. To this end, a fourth goal of the symposium was to bring together speakers not traditionally part of a single gathering to discuss results from diverse disciplines relevant to biogeography.

Consistent with these goals, the discussions begin with a summary of the biogeographic history of Gondwanan vertebrates by David Krause and others and a historical perspective of South American land mammals by Rosendo Pascual. The next papers focus on development of the land bridges that connect North and South America and the history of migrations across those bridges. Evolutionary biologist Blair Hedges summarizes current thinking about the evolution of the West Indian vertebrate fauna within that physical context, and S. David Webb reviews the Great American Biotic Interchange, bringing a lifetime of experience to interpreting the complex events that led to the formation of the Panamanian land bridge and to documenting the biological consequences of the union of South America with North America after 55 million years of separation.

More recent events and the biotic responses that modernized the landscape, environments, and communities of Latin America in the Quaternary are discussed in three papers. Sarah Metcalfe reviews information from spores, pollen, diatoms, rodent middens, dendrochronology, and deep sea cores to reconstruct fluctuations in climate for the northern deserts and the central Transvolcanic Belt of Mexico. Although the record is complex, Late Quaternary events, documented initially for the high latitudes, are shown to have affected northern and central Mexico, including a dry mid-Pleistocene, a more moist Holocene, and El Niño–Southern Oscillation (ENSO) cycles. In contrast to older views that conditions and communities became more stable and were essentially unchanged toward the tropics, a wealth of evidence

now documents that the climates and biotas at the lower latitudes had a dynamic and complex Quaternary history.

Human influence becomes a factor in shaping the biotas of lowland Central America by 20,000 yr. BP, and that history is recounted by Dolores Piperno using plant microfossils, charcoal, and, innovatively, a group of plant crystals called phytoliths and starch grains of agriculturally important plants preserved on grinding tools.

One long-standing barrier to the detailed reconstruction of Quaternary vegetation history from high altitudes in the tropics has been the lack of continuous or near-continuous records. Cores from which paleobiological information on terrestrial biotas are retrieved mostly extend back only to approximately 60,000 yr. BP or less, and rarely into the previous interglacial at 100,000 yr. BP. This means that records must be spliced together from different sites and studied through a variety of techniques. The results have been less-than-consistent accounts of the climatic, biotic, and uplift history for several regions of the Neotropics (e.g., the Atacama Desert and the high elevations of Chile and Bolivia; Grosjean et al., 2003; Baker et al., 2001). This limitation was removed for one site in northern South America when cores 357 m and 586 m long, dating to 1.6 million and 3 million years, respectively, were drilled through sediments of the interandean basins around Bogotá, Colombia. These cores were obtained by a group from the University of Amsterdam and their Colombian colleagues led by Henry Hooghiemstra. The history of páramo and montane vegetation is revealed in considerable detail from Funza, and these and other studies in the northern Andes are revealing abrupt, short-term fluctuations in climate such as the Little Ice Age, Younger Dryas, Heinrich, and Dansgaard-Oeschger events long recognized in sediments from the Northern Hemisphere.

The fullest understanding of tropical ecosystems will require a seamless integration of studies on their history with those on the existing temporal versions. This synthesis has yet to be fully achieved, but there is some information on the Quaternary Atlantic Forest of Brazil (Ledru et al., 2005). This will complement nicely the studies of Rodolphe Spichiger and others (e.g., Perret et al., this volume) on the biogeographic history of the Gesneriaceae in the Atlantic Forest via dispersal-vicariance analysis.

My own contributions on the geologic record of the Rhizophoraceae and on the origin of African–South American biotic affinities make two points not widely emphasized in the current biogeographic literature. With reference to the history of *Rhizophora* in the Caribbean region, it is clear from the extensive fossil pollen record that the genus first appears at the middle to late Eocene transition (ca. 45 million years ago) and has been more or less continually present ever since. One interpretation of the emerging molecular evidence is that, rather than distributional and taxonomic stasis, the genus disappeared for an estimated 3 million years between ca. 14 and 11 million years ago, and that the modern black mangroves are derived from progenitors that arrived ca. 11 million years ago. It is possible that both results are valid because the stenopalynous pollen establishes the presence of *Rhizophora*, as a genus, continuously in the region for 45 million years, but does not preclude the extinction and re-introduction of the molecular-defined extant lineages throughout this interval. A duality of stasis versus more dynamic change will likely become commonplace as paleobiogeographic patterns and evolutionary histories from the fossil record and from molecular data are compared.

My other contribution involves a synthesis of observations from different disciplines regarding the increasing number of elements that are recognized as having migrated between Africa and the Caribbean/South American region. This interchange has been accomplished in a variety of ways, including vicariance in Cretaceous and Paleocene times, expressed primarily at the higher taxonomic categories; direct overland migration across the North Atlantic land bridge until about the middle Eocene; and long-distance dispersal occurring throughout this time but becoming essential after about the middle Eocene. The relative importance of these overlapping modes depends on the dispersal potential of the propagules, the ecological requirements of the migrants, the time during which the lineage under consideration has been in existence, and the physiographic and climatic conditions prevailing in the region being transversed at the time the migrations occurred. Observations relevant to long-distance dispersal between Africa and South America are: (1) the enormous quantities of dust and organic debris being blown from the Sahara and Sahel into the Caribbean region, especially during periods of major hurricanes; (2) the increase in hurricane intensity, and possibly hurricane frequency, with global warming; and (3) the existence in the geologic past of intervals when global temperatures were considerably warmer than at present (e.g., during the early Eocene climatic optimum and in the middle Pliocene: Schmitz et al., 2000; Cronin & Dowsett, 1991). Furthermore, the Eocene was the time of emergence of the Greater Antilles, and the distance between Africa and South America was about one-half to one-third less than at present. Thus, the opportunity for wind transport for some organisms and/or their

propagules may have been greater during these peaks of warmth than would seem plausible under modern conditions. There are extant plant genera in which molecular evidence suggests disjunctions between Old World and New World taxa originated ca. 3–4 million years ago (viz., in the middle Pliocene; Graham, this volume).

Collectively, the papers of the symposium illustrate some of the past and present characteristics and affinities of the Latin American biota and the causes leading to its modernization. Interwoven throughout are examples of the various techniques being utilized to reveal their history. This record is becoming increasingly recognized as important to understanding the origin, development, and functioning of the present faunal and floristic communities and in anticipating future environmental and biotic change. To emphasize the considerable array of techniques available for investigating the historical aspects of ecosystems, the following list augments the approaches noted in the papers of this volume (see also Graham, 1999: chapter 4—Methods, Principles, Strengths, and Limitations):

(1) It is now possible to determine the concentration of CO_2 and other greenhouse gasses in the Earth's atmosphere over the past 100 million years, correlate the fluctuations with temperature trends based on oxygen isotope ratios, date the events through paleomagnetic and biostratigraphic studies, and relate the reconstructed climate to the history of lineages and communities. This is accomplished by such diverse techniques as analyzing gas in air bubbles trapped in ice and by calculating the changing mass of the Earth's carbonate sediments through time. It is also possible to calibrate the stomatal index of leaves from extant plants growing in environments of known CO_2 concentration, as well as from herbarium sheets, and to apply the indices to fossil cuticles of different ages. In this way, past concentrations can be estimated, and the fluctuations can be compared with temperature trends from oxygen isotope studies in the marine realm and with vegetational histories from the terrestrial environment.

(2) Changes in albedo (reflectivity), precipitation, carbon storage (sinks), and carbon release (pumps) can be estimated for various vegetation types (e.g., tundra, boreal forest, tropical rain forest, tropical savannas) and the climatic implication assessed as vegetation is cleared or as one vegetation type (e.g., lowland rain forest) is replaced by another (e.g., caatingas/cerrado) over geologic time. Alterations in plant cover are an important feedback to climate because, for example, half of the precipitation over the rain forest is generated by the forest itself (Clapperton, 1993).

(3) The amounts of insolation can be calculated for specific places and times as the Earth changes position relative to the sun (the Milankovitch cycles). It is also known that the solar constant (2 cal/cm^2/min) has varied over time, and although these fluctuations cannot be precisely quantified and do not seem to vary in concert with extinctions, evolutionary peaks, or migrational histories, they constitute a dampening or amplifying overlay to the Milankovitch variations and other climate-forcing mechanisms.

(4) The height of mountains at various points in time can be estimated by calculating the mean annual temperature of time-equivalent fossil floras from sea level and from high elevations using the modern analogue method and/or leaf margin analysis (Gregory-Wodzicki, 2000; Graham et al., 2001). By applying the average global lapse rate of 6 C/km, an approximation of the altitude of the highland flora can be made. These estimates, together with other geologic information, have revealed that about half the elevation of the Central Andes has been attained in relatively recent times (viz., since the late Miocene). That has implications for such topics as the time of origin of páramo environments and vegetation, speciation by vicariance in the region, and the migration of temperate and high-altitude organisms along the axis of the high Andes.

(5) The growth of stalagtites, and the midges and mites they often contain, is being used to estimate precipitation history in the deserts of the southeastern United States, in adjacent northern Mexico, and in Brazil (e.g., Polyak et al., 2001).

(6) Amino acid racemization in radiocarbon-dated emu eggshell fragments is a function of temperature, and it is being used to reconstruct climates in parts of the Southern Hemisphere (Johnson et al., 1999).

(7) Alkenones are long-chained organic molecules from algae that preserve in ocean sediments as biochemical fossils. The degree of unsaturation is temperature sensitive (increasing unsaturation indicates cooling water), and this affords a method of detecting El Niños during times beyond historical records. The modern cycle of El Niños along the Peruvian coast appears to have begun ca. 5800 yr. BP, and it corresponds to a time of intense monument building, while the onset of even stronger events corresponds to their abandonment.

(8) The solubility of noble gases is dependent on the temperature of the water, and ^{14}C-dated samples from groundwater in Brazil indicate a cooling of 5 C at the Last Glacial Maximum ca. 18,000 yr. BP. This is one example from a wealth of new information that indicates lowland Amazonia experienced significant cooling during the Quaternary. Whether it also experienced drying and, if so, when, where, and to what extent, is still unknown despite proclamations to the contrary in the much-debated issue of refugia.

(9) Titanium is a terrestrial mineral that is found in offshore basins of Venezuela. Decreases in the amounts along sections of marine cores reflect periods of reduced runoff and river flow, and it is one indication of aridity associated with cooling in Amazonia during intervals of the Quaternary.

(10) Geographical information systems (GIS) tools, remotely sensed data, and niche modeling techniques are being integrated with botanical data to study the ecology and evolution of plant geographic ranges and spatial patterns of diversity (Trisha Consiglio, Analysis Unit, Center for Conservation and Sustainable Development, Missouri Botanical Garden; pers. comm., 2006).

These and other techniques demonstrate how far we have come since the early great synthetic minds of

biology laid the foundations of biogeography. Linnaeus, through the 186 dissertations of the *Amoenitates Academicae*, noted that the vegetation of distant regions showed floristic similarities (e.g., Kamchatka and eastern North America in the 1750 dissertation of Jonas P. Halenius); that is, there were patterns in the arrangement of organisms over the landscape. Von Humboldt established in 1807, from his observations in the Ecuadorian Andes, that vertical changes in communities along mountain slopes were comparable to horizontal changes with latitude. He concluded that climate is an important factor in determining these patterns, and that did much to place the study of biogeography on a scientific basis. More recently, the consideration of time and the occurrence of past events has become increasingly recognized as an essential component of biogeography, as it was when geologist Lyell implanted the concept that lineages and communities extend back through time in the thinking of Darwin and Wallace on evolution. The papers presented here, and in other recent symposia, are a statement of the progress being made in understanding the causes and the implications of plant and animal distributions. The likes of Linnaeus, Von Humboldt, Darwin, and Lyell would undoubtedly be amazed and immensely pleased.

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LATE CRETACEOUS TERRESTRIAL VERTEBRATES FROM MADAGASCAR: IMPLICATIONS FOR LATIN AMERICAN BIOGEOGRAPHY[1]

David W. Krause,[2] Patrick M. O'Connor,[3] Kristina Curry Rogers,[4] Scott D. Sampson,[5] Gregory A. Buckley,[6] and Raymond R. Rogers[7]

Abstract

The Mahajanga Basin Project, initiated in 1993 and centered in Upper Cretaceous strata of northwestern Madagascar, has resulted in the discovery of some of the most complete, well-preserved, and significant specimens of Late Cretaceous vertebrate animals from the Southern Hemisphere and indeed the world. Among the most important finds are various specimens of crocodyliforms, non-avian dinosaurs, and mammals; these finds have the potential to provide key insights into the biogeographic and paleogeographic history of Gondwana. Madagascar has been physically isolated from Africa for over 160 million years and from all other major landmasses for more than 85 million years. The closest known relatives of many of the Late Cretaceous Malagasy taxa are penecontemporaneous forms from South America (primarily Argentina) and India, thus documenting a previously unrecognized high level of cosmopolitanism among Gondwanan vertebrates near the end of the Cretaceous. The family-level taxa that are shared among Madagascar, South America, and the Indian subcontinent are not known from penecontemporaneous horizons in mainland Africa, but it cannot yet be confidently determined if this is due to differential extinction, poor sampling, true absence (i.e., the taxa were never present on Africa), or some combination thereof. Nonetheless, currently available geologic and paleontologic data are most consistent with the Africa-first model, suggesting that Africa was the first of the major Gondwanan landmasses to be fully isolated prior to the Albian/Cenomanian boundary, and that its terrestrial vertebrate faunas became progressively more provincial during the Cretaceous, while those on other Gondwanan landmasses remained relatively cosmopolitan until the later stages of the Late Cretaceous.

Key words: biogeography, Cretaceous, Madagascar, South America, vertebrates.

Resumen

El proyecto de la cuenca de Mahajanga, iniciado en 1993 y centrado en los estratos del Cretácico superior en el noroeste de Madagascar, ha resultado en el descubrimiento de algunos de los especímenes más completos, mejor preservados y más significativos de animales vertebrados del Cretácico tardío del hemisferio sur y de hecho del mundo. Entre los hallazgos más importantes son los varios especímenes de crocodiliformes, dinosaurios no-aviares y mamíferos; estos hallazgos tienen el potencial de adentrarse en puntos claves en la historia biogeográfica y paleogeográfica de Gondwana. Madagascar ha estado físicamente aislada de África por más de 160 millones de años y del resto de masas importantes de tierra por más de 85 millones de años. Los parientes cercanos conocidos de muchos de los taxones malgaches del Cretácico tardío son formas penecontemporáneas de América del Sur (sobre todo de Argentina) y la India, documentando así un alto nivel cosmopolita previamente desconocido entre los vertebrados de Gondwana cerca del final del Cretácico. Los taxones al nivel de familia compartidos entre Madagascar, América del Sur y el subcontinente Indio no se conocen de horizontes penecontemporáneos de África continental, pero todavía no se puede determinar con certeza si esto se debe a extinción diferenciada, escaso muestreo, ausencia verdadera (i.e., los taxones nunca estuvieron presentes en África), o una cierta combinación de esos. No obstante, los datos geológicos y paleontológicos actualmente disponibles son los más consistentes con el modelo de África primero, que sugiere que África fue la primera de las masas importantes de tierra de Gondwana que estuvo aislada completamente antes del límite del Albiano/Cenomaniano, y que su fauna de vertebrados terrestres se volvió progresivamente más provincial durante el Cretácico mientras que aquellos en las masas terrestres de Gondwana permanecieron relativamente cosmopolitas hasta las fases finales del Cretácico tardío.

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The first question that logically might occur to readers of this contribution is "Why is Madagascar relevant to a consideration of Latin American biogeography?" The answer is not intuitively obvious because over 7500 km separate the two landmasses today and Madagascar's extant biota is highly endemic and imbalanced. However, in the context of a mobilist paradigm of Earth history, the question has different degrees of relevance depending upon the geologic time interval under consideration. We will assert in this paper that near the end of the Late Cretaceous the island-continent of Madagascar hosted a terrestrial vertebrate fauna that was strikingly similar in taxonomic composition to that of South America. This high degree of similarity is unexpected in the context of most recent paleogeographic reconstructions, which depict the southern supercontinent Gondwana as having long been fragmented into its constituent landmasses by this time. Specifically, Madagascar, although still connected to the Indian subcontinent, is usually illustrated as having been physically isolated from all other Gondwanan landmasses since approximately 120 million years ago (Ma). This presents a biogeographic conundrum, as noted by Hay et al. (1999).

The configuration of Gondwana changed dramatically during the Late Jurassic and Cretaceous as it broke apart into isolated landmasses. The dispersion of these landmasses undoubtedly had profound consequences for the geographic distribution and subsequent evolutionary trajectories of the resident terrestrial vertebrate faunas. Reconstructions of the Mesozoic fragmentation of Gondwana, however, are based almost exclusively on geophysical and stratigraphic evidence and remain poorly tested paleontologically. Recent discoveries of fossil vertebrates on southern landmasses, particularly from the Late Cretaceous of Madagascar (cf. Krause et al., 1999; Krause, 2003b), complement those known from South America and elsewhere and have profound implications for testing hypotheses concerning the timing and sequence of Gondwanan breakup. Purportedly isolated in the Indian Ocean for over 85 million years, Madagascar is of unique biogeographic importance; it occupied a central geographic position within Gondwana and was among the first (western margin) and last (eastern margin) major landmasses to be involved in fragmentation of the supercontinent.

The objective here is to provide an overview of the terrestrial vertebrate assemblage recently recovered from the latest Cretaceous stage (Maastrichtian) of Madagascar and to compare it with penecontemporaneous and earlier assemblages from South America and other Gondwanan landmasses in an attempt to elucidate biogeographic patterns. Terrestrial vertebrates are the focus of this report because they are tied to land (some presumably more than others) and are thus the most appropriate vertebrate animals (i.e., relative to, for example, fishes or birds) for examining biogeographic hypotheses involving subaerial landmasses. We specifically focus on crocodyliforms, non-avian dinosaurs, and mammals for the simple reason that their representation in the Gondwanan terrestrial fossil record is better than for most other terrestrial vertebrate clades and, as a result, their phylogenetic relationships are more highly resolved. This report is not a comprehensive analysis of Gondwanan biogeography. Rather, it is an attempt to compare and evaluate the currently available data provided by terrestrial vertebrate fossils from major southern landmasses, particularly Madagascar and South America, in the context of recent paleogeographic reconstructions of Gondwana. We also strive to identify and draw attention to sampling problems that limit our ability to address particular biogeographic questions.

Terrestrial Vertebrates from the Latest Cretaceous of Madagascar

The sample of latest Cretaceous (Maastrichtian) vertebrates from Madagascar is the most diverse and arguably the most significant in terms of completeness and preservation of specimens among Gondwanan assemblages outside of South America. This is particularly striking considering the small size of Madagascar; indeed, mainland Africa, the largest of the Gondwanan landmasses, is over 50 times larger in area and yet its penecontemporaneous vertebrate fauna is much more poorly known.

The vast majority of specimens known from the Late Cretaceous of Madagascar have been discovered as a result of the Mahajanga Basin Project (MBP), conducted jointly by Stony Brook University and the University of Antananarivo. The MBP was initiated in 1993 and has included eight expeditions, the most recent in 2005. It is focused on the vertebrate paleontology and geology of Upper Cretaceous strata in the Mahajanga Basin of northwestern Madagascar (Fig. 1). Most of the fossil vertebrate specimens have been recovered from a small study area (measuring approximately 20 sq. km) near the village of Berivotra and from one thin stratigraphic interval (measuring some 12 m thick). Existing stratigraphic data indicate that this interval, the Anembalemba Member of the Maevarano Formation, is of Maastrichtian (latest Cretaceous) age; however, we cannot discount the possibility that lower reaches of the member might be Campanian (Rogers et al., 2000). The Anembalemba Member is of fluvial origin and accumulated in a semi-

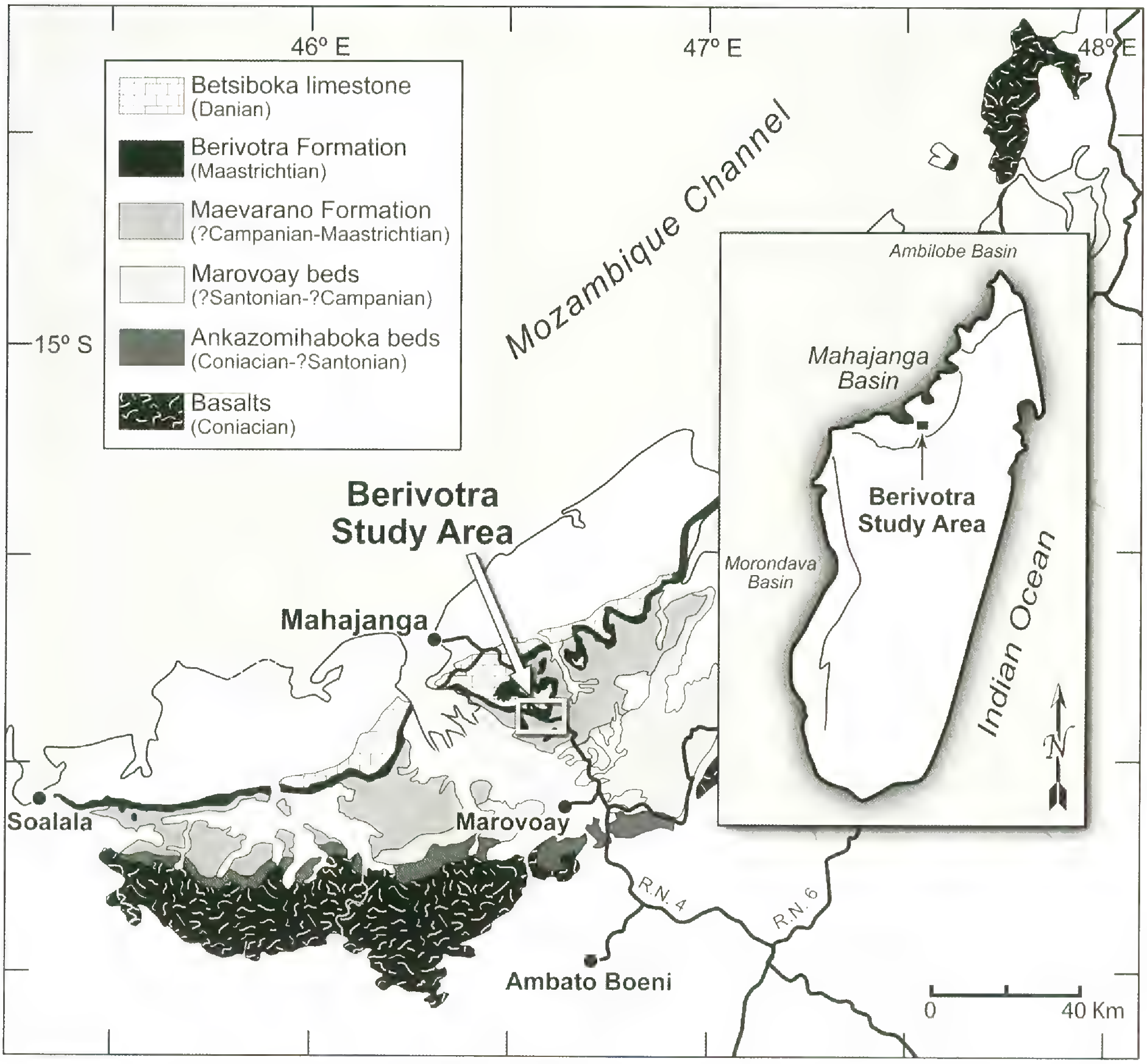

Figure 1. The Berivotra Study Area in the Mahajanga Basin of northwestern Madagascar and the outcrop area of Upper Cretaceous and Paleocene strata in the basin. Question marks indicate uncertainty concerning age estimations.

arid setting characterized by repetitive flood events that triggered fine-grained debris flows. These debris flows in turn served to entomb and preserve massive quantities of vertebrate skeletal material (Rogers et al., 2000; Rogers, 2005).

Our ongoing efforts have dramatically increased the previously known (pre-1993) species diversity of Late Cretaceous vertebrates from the island (cf. Krause et al., 1997a, 1999; Krause, 2003b). The fauna is now known to include fishes, frogs, turtles, lizards, snakes, crocodyliforms, non-avian dinosaurs, birds, and mammals. Many new genera and species have been discovered and many of the higher taxa represented are the first documented occurrences for the pre–Late Pleistocene of Madagascar (e.g., frogs (Asher & Krause, 1998), lizards (Krause et al., 2003a), birds (Forster et al., 1996), mammals (Krause et al., 1994)). Furthermore, some of the higher taxa represent the *only* known occurrences from Madagascar, fossil or Recent (e.g., gondwanatheres (Krause et al., 1997b) and marsupials (Krause, 2001) among mammals), and some represent the first Late Cretaceous records from large portions of Gondwana (e.g., lizards, birds, marsupials).

Study of these vertebrate fossils and the sediments that encase them provides important information on the anatomy, paleobiology, ecology, and phylogenetic relationships of several vertebrate higher taxa and has resulted in important insights into, among other topics, the origin and early evolution of birds (Forster et al., 1996, 1998, 2003; Forster & O'Connor, 2000; Chinsamy & Elzanowski, 2001); the Gondwanan diversification and distribution of crocodyliforms (Buckley et al., 1997, 2000; Buckley & Brochu, 1999; Rasmusson, 2002; Rasmusson & Buckley, 2001; Turner, 2004a, b), saurischian dinosaurs

Table 1. Crocodyliform genera from the Anembalemba Member of the Maevarano Formation, Upper Cretaceous (Maastrichtian), Mahajanga Basin, Madagascar.

Mesoeucrocodylia
Metasuchia
Notosuchidae
Simosuchus Buckley, Brochu, Krause & Pol
Peirosauridae
Genus indet.
Trematochampsidae
Trematochampsa Buffetaut & Taquet
Metasuchia *incertae sedis*
Araripesuchus Price
Mahajangasuchus Buckley & Brochu
Genus indet. A
Genus indet. B

(Sampson et al., 1998, 2001; Curry Rogers & Forster, 2001, 2004; Curry Rogers, 2002, 2005; Carrano et al., 2002, 2004; O'Connor & Claessens, 2005; O'Connor, in press), and mammals (Krause et al., 1997b; Krause, 2001); the biogeographic origins of the highly endemic extant Malagasy vertebrate fauna (Krause et al., 1997a, 1999; Krause, 2003b); and the stratigraphy, sedimentology, and geochronology of Upper Cretaceous rocks in the Mahajanga Basin (Krause & Hartman, 1996; Rogers et al., 2000, 2001; Casey et al., 2003; Rogers, 2005). Perhaps most significantly, these discoveries have profound implications for testing biogeographic hypotheses that, in turn, address broader questions concerning the timing and sequence of Gondwanan fragmentation (Krause et al., 1997a, b, 1999; Sampson et al., 1998; Krause, 2003b).

The record of Late Cretaceous terrestrial vertebrates from Gondwana is spotty at best and therefore difficult to analyze and interpret in a biogeographic context. Among the vertebrate groups represented in the Late Cretaceous of Madagascar, the best known in terms of their completeness and preservation and therefore the most precisely identified, are the crocodyliforms, non-avian dinosaurs, and mammals. These taxa are therefore the most relevant for consideration of biogeographic relationships. The following provides a brief overview of the taxonomic and anatomical diversity of each of these taxa.

CROCODYLIFORMS

At least seven species of crocodyliforms, all metasuchians, are present in the Maevarano Formation (Table 1). This diversity is extraordinary, and it is therefore not surprising that a range of adaptations suggestive of habitat specialization is evident. In addition to extreme differences in body size and form, ranging from small and gracile to large and ponderous, there is a broad range in skull shape, from robust and broad to long and slender to short and blunt.

Mahajangasuchus insignis (Fig. 2), originally described on the basis of a nearly complete skeleton lacking only the skull, is the first crocodyliform genus and species from the Late Cretaceous of Madagascar to be named on the basis of MBP discoveries (Buckley & Brochu, 1999). Since publication on this specimen, two nearly complete skulls have been discovered (Buckley & Brochu, 2001). *Mahajangasuchus* was a large carnivore, measuring almost 4 m in length, and is distinctive among crocodyliforms in exhibiting an extremely broad and flat, hippopotamus-like snout and deep lower jaw.

Simosuchus clarki (Fig. 3) is a new, bizarre, pug-nosed species represented by a complete skull and articulated anterior half of a postcranial skeleton that were preliminarily described by Buckley et al. (2000). The blunt, shovel-like snout, deep cranium, posteroventrally positioned occipital condyle, underslung lower jaw, and areas for extensive neck musculature are suggestive of burrowing adaptations, whereas the anteriorly positioned jaw joint and clove-shaped teeth may reflect adaptations for herbivory (Fig. 3).

A new species, *Araripesuchus* sp. indet., is being described by A. Turner (in press). It is known from skulls and skeletons of at least five individuals, all recovered from a single locality, that reveal a small, gracile-limbed form (Fig. 4). *Araripesuchus tsangatsangana* represents the geologically youngest occurrence, yet most primitive known member of the genus (Turner, 2004a, b; in press).

Trematochampsa oblita Buffetaut & Taquet, named on the basis of three fragmentary dentaries, is the only crocodyliform species from the Late Cretaceous of Madagascar that was described prior to inception of the MBP (Buffetaut & Taquet, 1979). A better-preserved dentary, as well as several skull and postcranial elements, were recovered by MBP expeditions (Rasmusson & Buckley, 2001). The new material of *T. oblita* provides the opportunity for a better understanding of phylogenetic relationships of trematochampsids; Rasmusson (2002) determined that trematochampsids are monophyletic, but that the genus *Trematochampsa* is paraphyletic. Although still poorly known, it is clear that *T. oblita*, like *Mahajangasuchus*, was a massive animal and likely one of the top predators of its time.

In addition to these named crocodyliform taxa, there are at least three as yet unnamed species recovered from the Maevarano Formation. One is represented by several skull elements preliminarily identified as peirosaurid. The second is a medium-sized (i.e., smaller than *Mahajangasuchus insignis* and

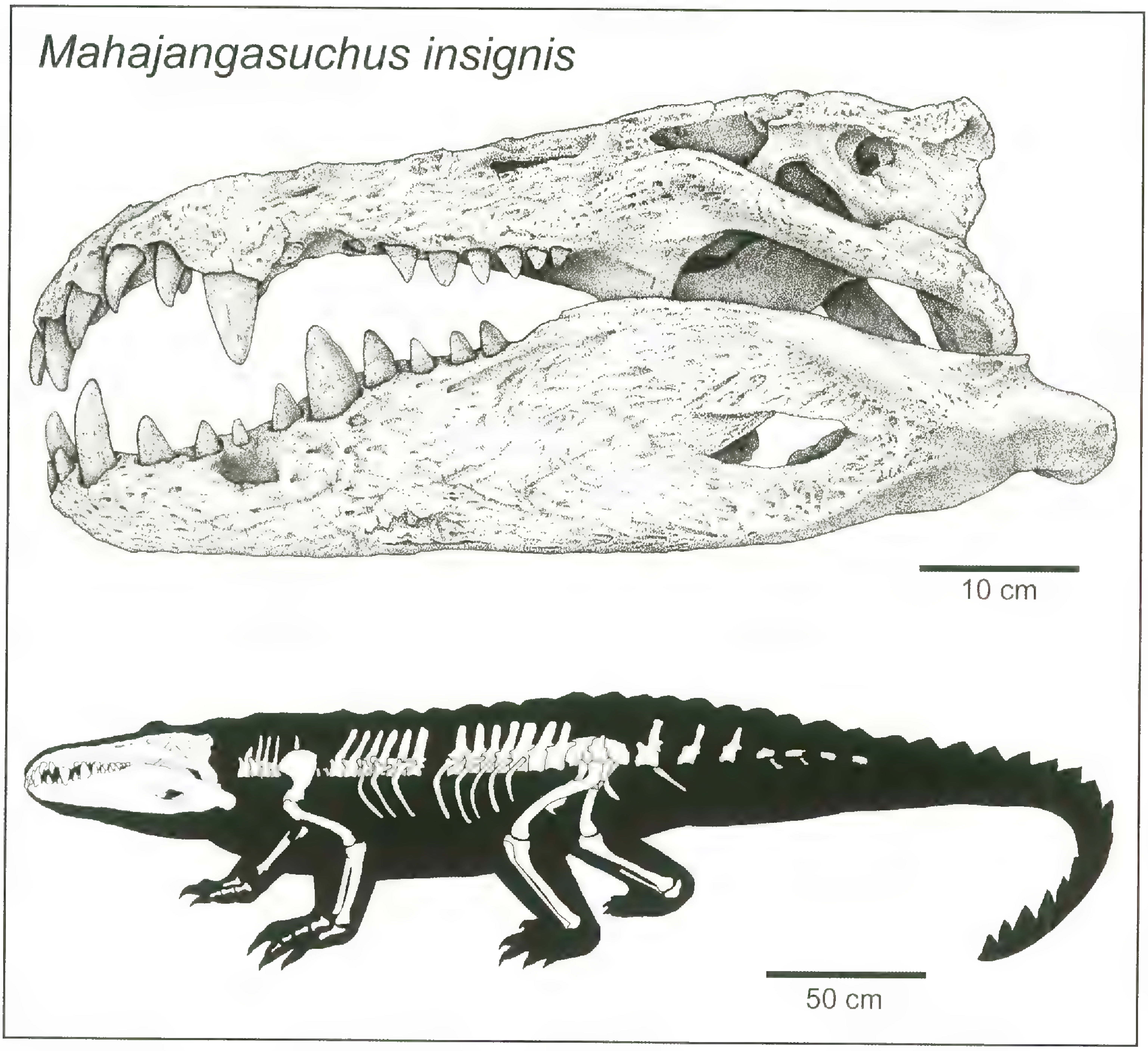

Figure 2. *Mahajangasuchus insignis* Buckley & Brochu, a large, broad-mouthed metasuchian crocodyliform from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

Trematochampsa oblita, but larger than *Araripesuchus* sp. indet.), slender-snouted metasuchian, represented by a partial skull, a complete lower jaw, and considerable postcranial material (Buckley et al., 2003). The third is poorly known, represented only by isolated elements, primarily partial skull and jaw material.

NON-AVIAN DINOSAURS

Dinosaur material is abundant in the Maevarano Formation, but to date is limited to the Saurischia. At least four non-avian species have been discovered: two theropods and two sauropods (Table 2).

The best represented of the two theropods is the mid-sized (approximately 6.2 m in length) abelisaurid *Majungatholus atopus*, previously thought to be a pachycephalosaurid ("dome-headed" ornithischian dinosaur) based on fragmentary skull material (Sues & Taquet, 1979; Sues, 1980; Fig. 5). One of the most spectacular fossil discoveries of the MBP to date is an exquisitely preserved and virtually complete skull and lower jaws of *M. atopus*, discovered in 1996 (Sampson et al., 1998). The short and deep skull bears fused nasal bones with a large interior pneumatic chamber, and a midline projection or "horn" positioned above the eyes, with a notable parietal eminence capping the skull roof posteriorly. Complementing this specimen are several other, more fragmentary, and less well-preserved skulls discovered recently, in addition to three partial skeletons, one of them representing a juvenile individual; thus, virtually all bones of the skeleton are now represented for this animal (the primary exceptions being parts of the pelvis and the distal portions of the forelimbs). These specimens confirm referral of *Majungatholus* to the Abelisauridae and are described in detail in a monograph-length study (Sampson & Krause, in

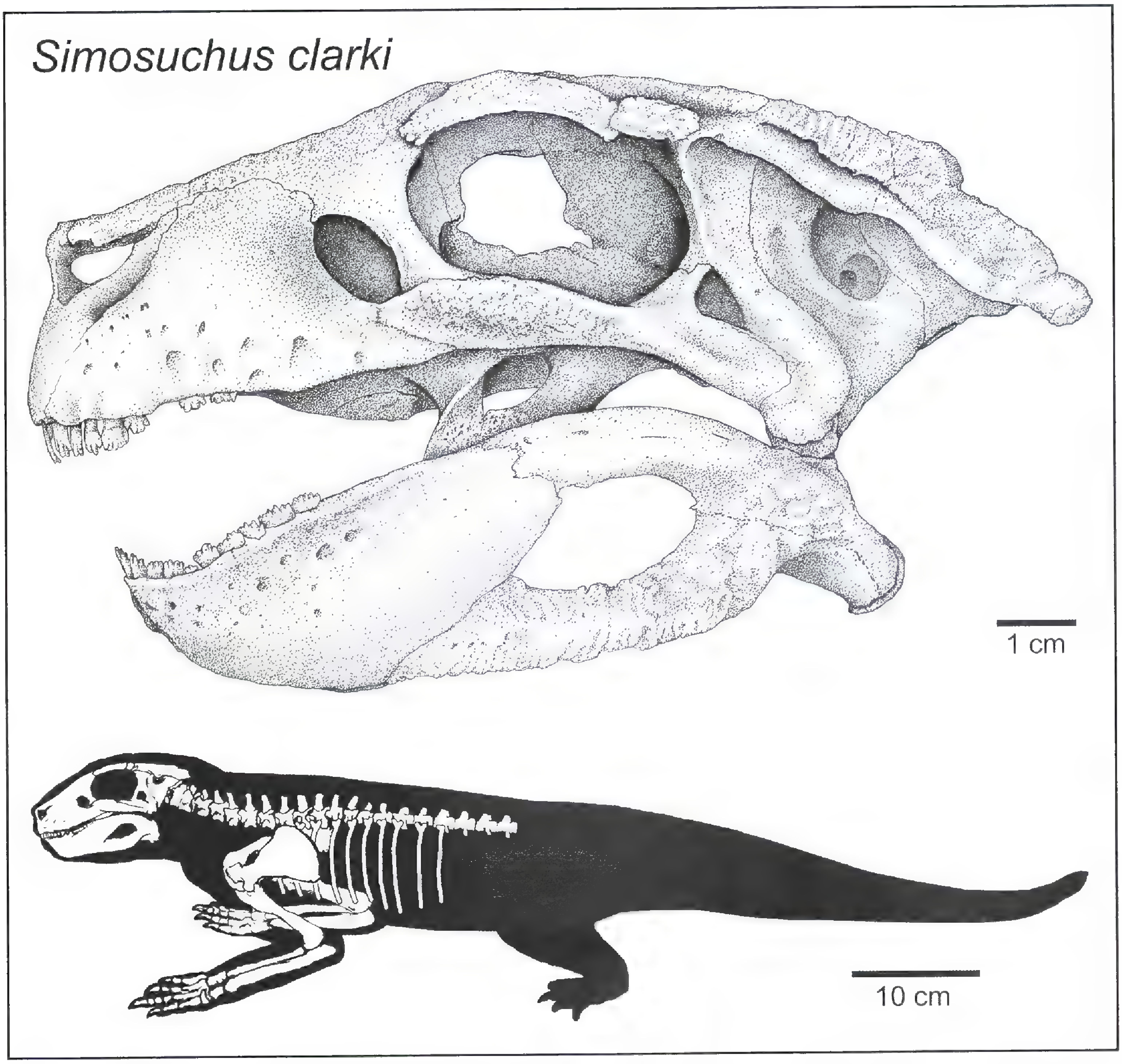

Figure 3. *Simosuchus clarki* Buckley, Brochu, Krause & Pol, a small- to mid-sized metasuchian crocodyliform from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

press). Numerous bones in the Maevarano assemblage exhibit tooth marks (some of which even preserve denticle drag marks) that can be attributed only to *Majungatholus*, thus attesting to its carnivorous habits. Interestingly, many of the bones are those of *Majungatholus* itself, thereby providing the first well-documented evidence for cannibalism among dinosaurs (Rogers et al., 2003).

Masiakasaurus knopfleri, measuring approximately 1.8 m long, was a much smaller and more gracile predator than *Majungatholus atopus* (Fig. 6). It is represented by isolated bones of both the skull and postcranial skeleton and is thus less completely known. *Masiakasaurus* is remarkable, however, in having an anterior dentition that consists of procumbent, spearing teeth, a unique condition among Dinosauria. *Masiakasaurus* was described by Sampson et al. (2001) and Carrano et al. (2002), who concluded that this Malagasy taxon should be included within the small-bodied abelisauroid clade Noasauridae, previously known only from Argentina. The placement of *Masiakasaurus*—together with the penecontemporaneous Indian form *Laevisuchus*—into Noasauridae (previously known only from Argentina) therefore greatly expanded the geographic range of this clade to encompass much of Gondwana. This finding demonstrates that, at least in a number of ecosystems, noasaurid abelisauroids were small-bodied counterparts to their larger-bodied cousins, the abelisaurids, in a manner parallel to small-bodied maniraptoran coelurosaurs (e.g., troodontids, oviraptorosaurs, dromaeosaurids) and large-boded tyrannosaurids in many Late Cretaceous Laurasian ecosystems. Recent fieldwork in 2003 and 2005 has produced additional

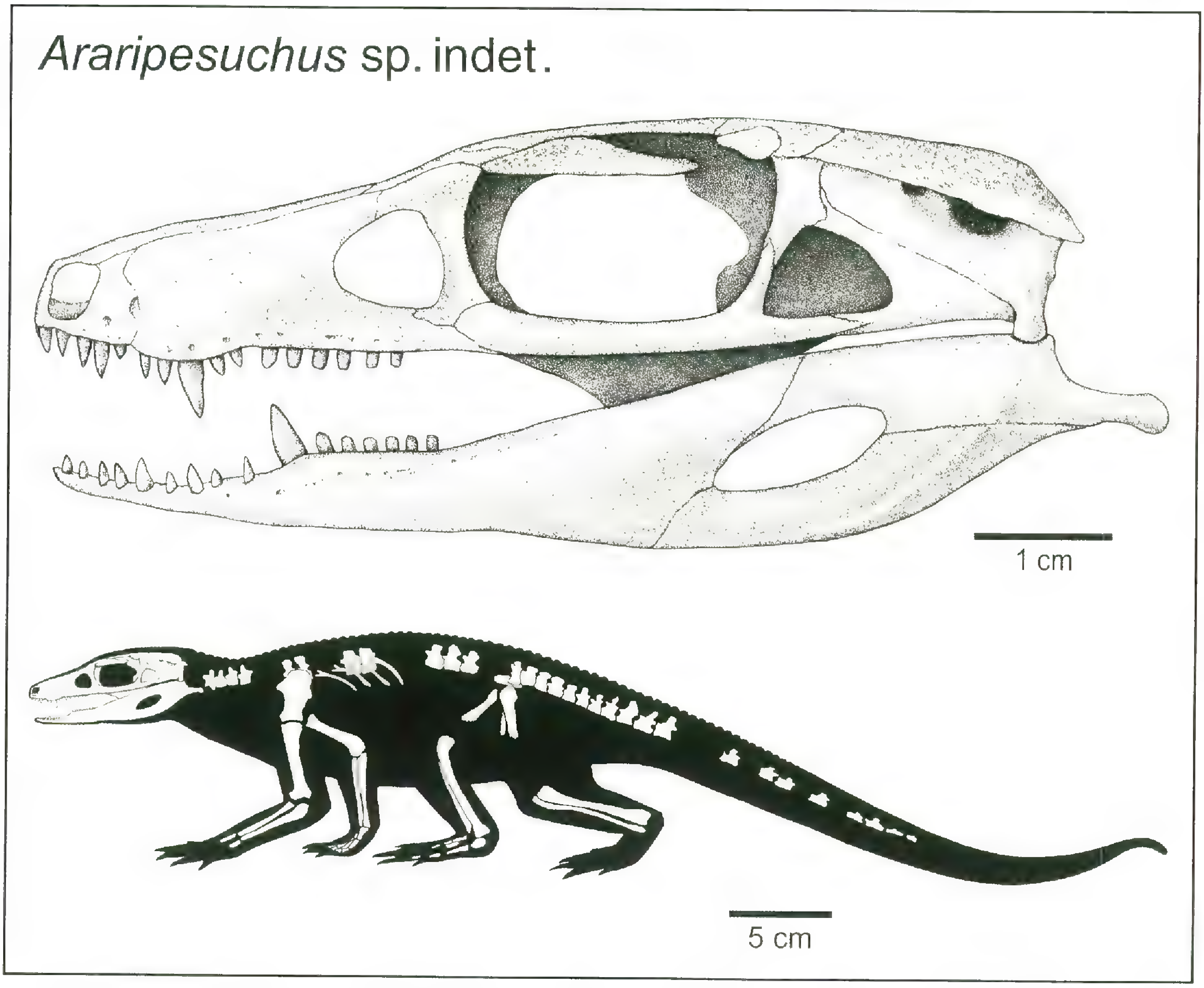

Figure 4. *Araripesuchus* sp. indet., a small, gracile-limbed metasuchian crocodyliform from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

skeletal remains of *Masiakasaurus*, including several key, previously unrepresented cranial and postcranial elements that will significantly increase knowledge of noasaurid anatomy (Carrano et al., 2004, in prep.).

Table 2. Non-avian dinosaur genera from the Anembalemba Member of the Maevarano Formation, Upper Cretaceous (Maastrichtian), Mahajanga Basin, Madagascar.

Theropoda
Ceratosauria
Abelisauroidea
Abelisauridae
Majungatholus Sues & Taquet
Noasauridae
Masiakasaurus Sampson, Carrano & Forster
Sauropoda
Titanosauria
Lithostrotia
Saltasauridae
Genus indet. (Malagasy Taxon B of Curry Rogers, 2002)
Lithostrotia *incertae sedis*
Rapetosaurus Curry Rogers & Forster

Titanosaurian sauropods were among the first fossils described from Madagascar and are abundant components of the Late Cretaceous fauna. At least two species of lithostrotian titanosaurs are present in the fauna, and at least one possessed osteoderms ("skin bones") that range in size from small ossicles to bony plates greater than 40 cm in diameter (Depéret, 1896; Dodson et al., 1998).

Rapetosaurus krausei is known from approximately 90% of its skeleton, including several well-preserved associated specimens representing a range of ontogenetic stages (Curry Rogers & Forster, 2001, 2004; Curry Rogers, 2005; Fig. 7). *Rapetosaurus* is particularly significant because it preserves cranial and postcranial data key to elucidating phylogenetic relationships among one of the most temporally and geographically widespread of dinosaurian groups. *Rapetosaurus* has already provided the first cranial data in support of Titanosauriformes monophyly and has helped to increase resolution of lower-level titanosaurian relationships (Curry Rogers & Forster, 2001; Curry Rogers, 2005).

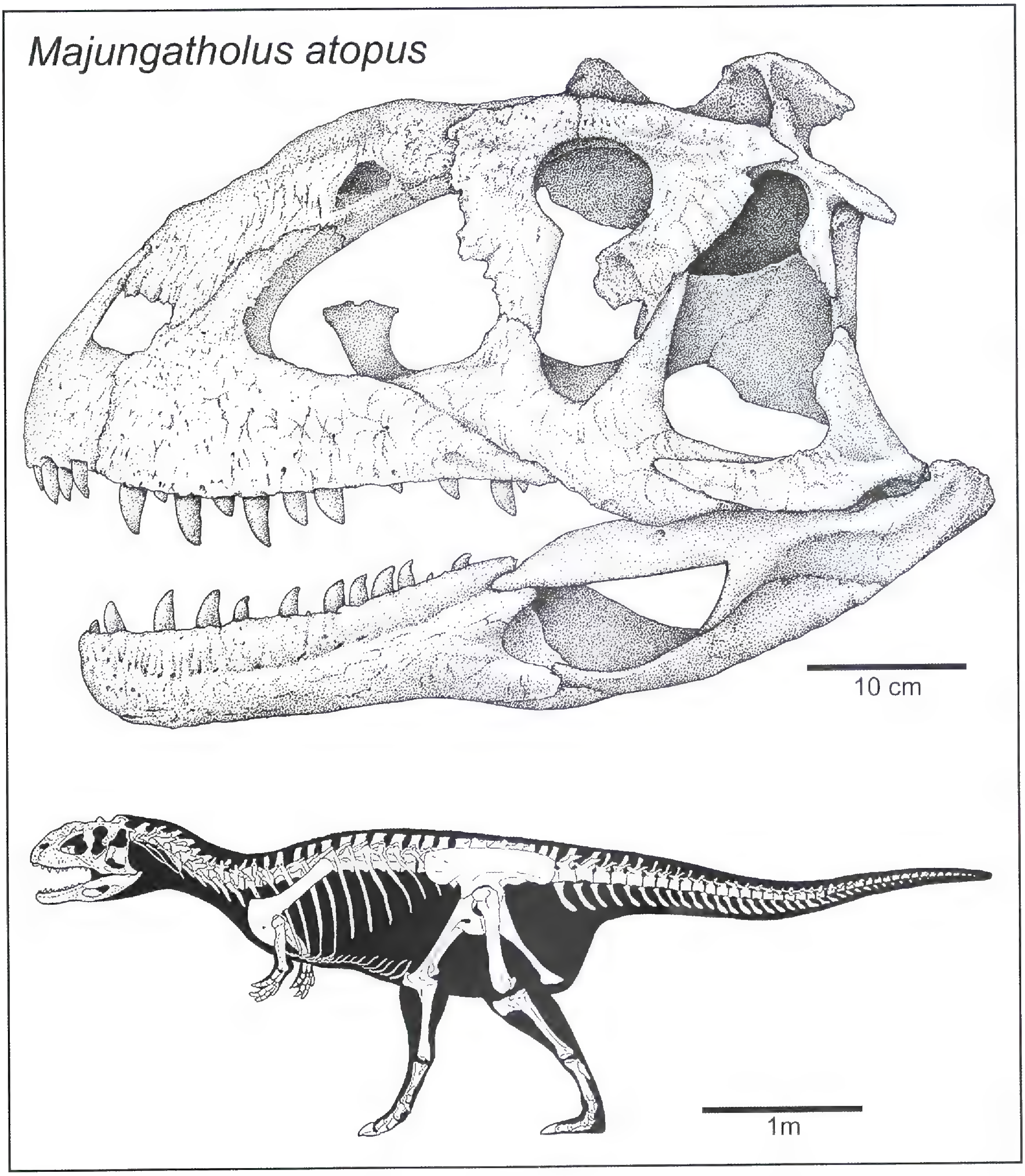

Figure 5. *Majungatholus atopus* Sues & Taquet, a mid-sized theropod dinosaur from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

"Malagasy Taxon B" (Table 2) is the second titanosaur species from Madagascar. Although represented by only several isolated caudal vertebrae, a series of articulated distal caudals, and an isolated coracoid (Curry Rogers, 2002, 2005), Taxon B can be easily distinguished from *Rapetosaurus*. The caudal centra of Malagasy Taxon B are distinctively dorsoventrally compressed and subrectangular in transverse section. In contrast, *Rapetosaurus* caudal centra have subequal height and width dimensions resulting in a round transverse section. Coracoids are also diagnostic: Malagasy Taxon B exhibits a square coracoid with broad scapular facet, whereas *Rapetosaurus* has a rounded coracoid with narrow scapular articulation.

Curry Rogers (2005) recently conducted a phylogenetic analysis and concluded that Malagasy Taxon B and *Rapetosaurus* are distant relatives within Titanosauriformes (Curry Rogers, 2005). Even more significantly, the compressed caudal vertebrae and low neural spines of Malagasy Taxon B indicate that it is a member of Saltasaurinae (sensu Wilson & Upchurch, 2003) with close affinities to the South

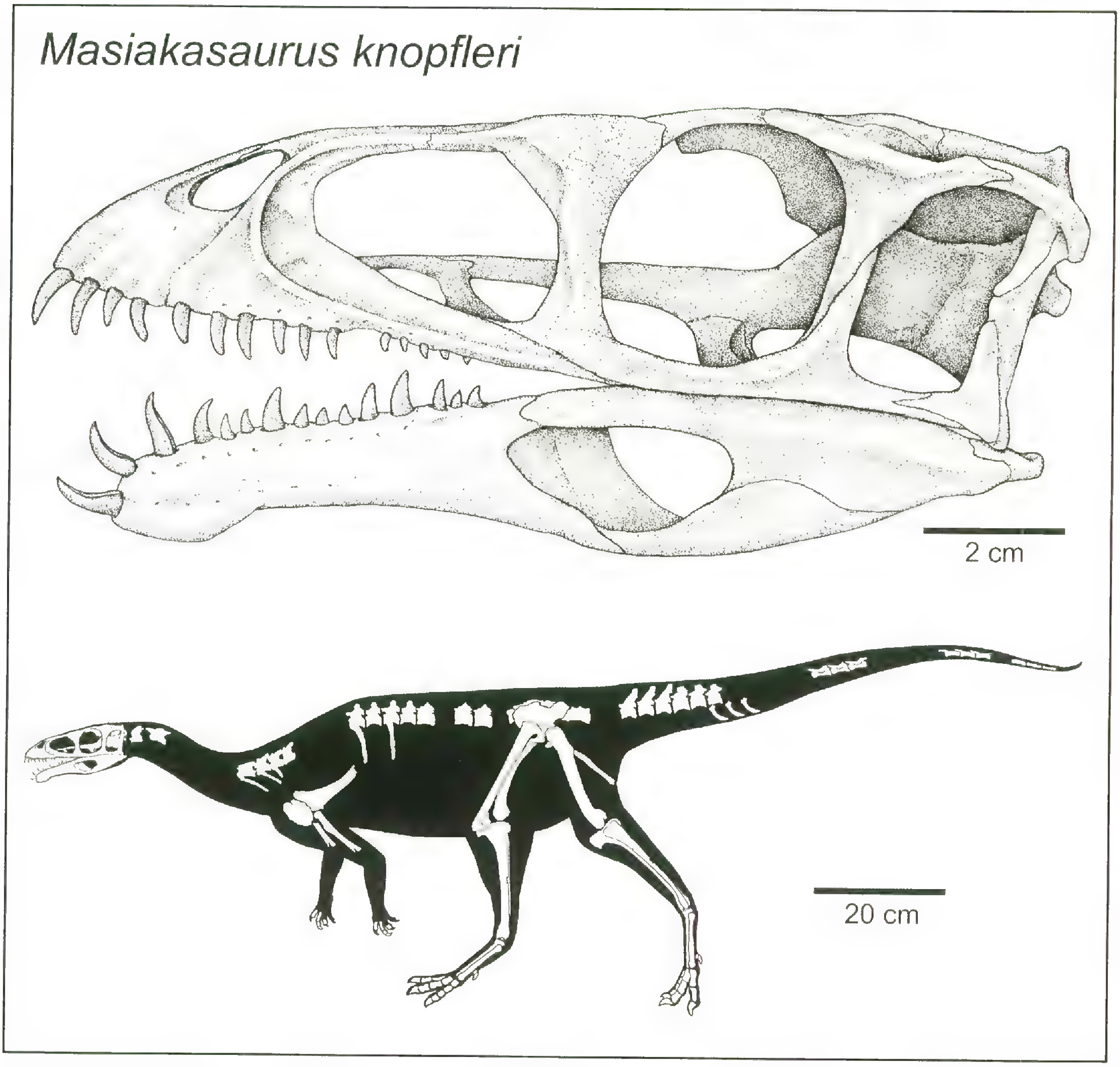

Figure 6. *Masiakasaurus knopfleri* Sampson, Carrano & Forster, a small theropod dinosaur from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

American saltasaurine genera *Saltasaurus*, *Neuquensaurus*, and *Rocasaurus*.

MAMMALS

The Late Cretaceous mammalian fauna of Madagascar is still poorly understood. It is represented by five, or perhaps six, taxa, each known from nothing more than a fragmentary tooth or two (Krause et al., 1994, 1997b; Krause & Grine, 1996; Krause, 2001, 2002; Table 3). One still-undescribed taxon, however, is represented by a nearly complete, well-preserved, and articulated skeleton (Krause, 2003a). Interestingly, none of the known taxa can be considered to be potential ancestors of the island's highly endemic extant mammalian fauna, all of which are placentals.

Two fragmentary mammalian teeth were assigned to a new genus and species, *Lavanify miolaka* Krause, Prasad, von Koenigswald, Sahni & Grine, a sudamericid gondwanathere (Krause et al., 1997b). Sudamericids are unique among Mesozoic mammals in possessing hypsodont cheek-teeth separated from gliriform incisors by a pronounced diastema. Just as for noasaurid theropods (see above), the discovery of sudamericids in Madagascar and the Indian subcontinent considerably extended the geographic range of the clade (previously known only from Argentina) and provided evidence for a previously unknown high degree of cosmopolitanism that encompassed both western and eastern Gondwana (see below).

At least one other tooth may also be assigned to Gondwanatheria (listed as Mammalia *incertae sedis* Genus indet. A in Table 3), although it is much larger and considerably lower crowned than those assigned to *Lavanify* (Krause, 2000). Still less high-crowned is another isolated tooth that exhibits a complex occlusal

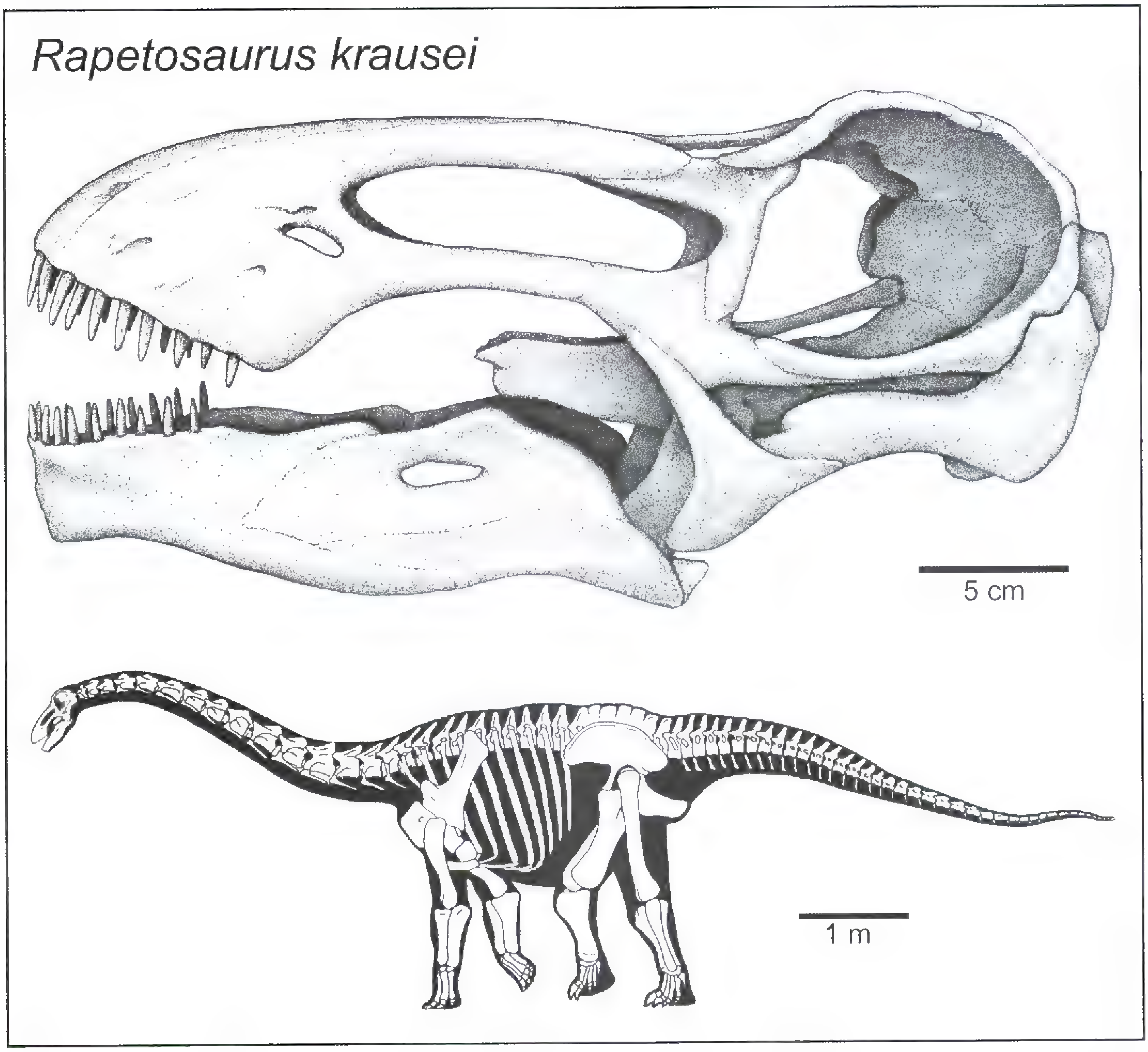

Figure 7. *Rapetosaurus krausei* Curry Rogers & Forster, a titanosaurid sauropod dinosaur from the Late Cretaceous of Madagascar. Subadult skull in left lateral view and restoration of the skull and skeleton in left lateral view.

morphology (W-shaped ridge with two infundibula separating each of the three limbs of the W) on an obliquely-oriented surface. This specimen could conceivably also pertain to Gondwanatheria but, based on current information, it could equally well belong to a previously unrecognized higher taxon of Mesozoic mammals.

Table 3. Mammalian genera from the Anembalemba Member of the Maevarano Formation, Upper Cretaceous (Maastrichtian), Mahajanga Basin, Madagascar.

Mammalia
Multituberculata
Genus indet.
Marsupialia
Genus indet.
Gondwanatheria
Sudamericidae
Lavanify Krause, Prasad, von Koenigswald, Sahni & Grine
Mammalia *incertae sedis*
Genus indet. A
Genus indet. B

Another isolated tooth, a tribosphenic lower molar, was regarded by Krause (2001) as that of a marsupial and therefore as potentially the earliest evidence of marsupials in the Southern Hemisphere. This identification was confirmed by Case and Krause (2002), but has since been disputed by Averianov et al. (2003); Case (in prep.) is nearing completion of a more detailed analysis that supports the marsupial affinities of the taxon represented by this specimen.

Another isolated specimen is a molar fragment exhibiting cusp-in-line morphology characteristic of multituberculates, a clade that is well represented and extremely diverse in penecontemporaneous, as well as earlier and later, horizons in Laurasia (Krause & Grine, 1996). Multituberculates are poorly known from the Mesozoic of the Southern Hemisphere, previously found

only in the Early Cretaceous of Morocco (Sigogneau-Russell, 1991; Hahn & Hahn, 2003) and possibly the Late Cretaceous (Campanian or early Maastrichtian) of Argentina (Kielan-Jaworowska et al., 2004).

Finally, one recently discovered taxon (listed as Mammalia *incertae sedis* Genus indet. B in Table 3) is represented by a virtually complete, articulated, subadult skeleton (Krause, 2003a). This skeleton, still in the process of being prepared and studied, represents the largest and most complete specimen of a mammal yet known from the Mesozoic of Gondwana. It exhibits a striking mosaic of primitive (e.g., septomaxilla with prominent septomaxillary canal, epipubic bone) and derived (e.g., specialized dentition with prominent diastema, well-developed humeral trochlea, reduced fibular-calcaneal contact) features. There is no doubt that this specimen will introduce a substantial amount of character conflict into previous topologies of mammalian phylogeny. It is also safe to conclude, even at this preliminary stage, that this animal cannot be "shoehorned" into any currently recognized higher taxon of mammals; it represents a major new nontherian clade. The relative completeness of this extraordinary specimen promises to elucidate the anatomy, functional morphology, and phylogenetic position of the clade it represents.

TERRESTRIAL VERTEBRATES FROM THE ANKAZOMIHABOKA SANDSTONES

Terrestrial vertebrate fossils have also been recovered from the Ankazomihaboka sandstones, a unit that is purportedly interbedded with, and definitely overlies, basalts of Coniacian age (Besairie, 1972; Storey et al., 1995, 1997). A preliminary report (Curry, 1997) indicates the presence of at least three crocodyliform taxa and two to three taxa of nonavian dinosaurs, including sauropods and theropods; no mammals were found. Subsequent collections have been made and a more extensive analysis of the assemblage from this unit is under way (Curry Rogers et al., in prep.). The taxa derived from the Ankazomihaboka sandstones are not considered here because of the tentative nature of the current identifications and because the age of the rock unit has not been ascertained, although, conservatively, it can be constrained to have been as early as Coniacian and as late as Maastrichtian.

Campanian/Maastrichtian Crocodyliforms, Non-Avian Dinosaurs, and Mammals from Other Gondwanan Landmasses

The primary purpose of this section is to compare the latest Cretaceous terrestrial vertebrate assemblages of Madagascar and South America. However, the taxonomic similarities between the assemblages from these two landmasses at the end of the Cretaceous make it clear that physical and biotic connections with other landmasses were also involved and must be considered. An overview of penecontemporaneous terrestrial faunas from potentially connected landmasses—namely Antarctica, Africa, and the Indian subcontinent—is therefore warranted. Australia and southern Europe also contained Gondwanan-aspect faunas during the Late Cretaceous, but there is no independent evidence indicating that either was *directly* connected to Madagascar or South America during this interval; as such, and owing to space considerations, their faunas are not considered here.

The faunal lists in Tables 4–6 provide an overview of the generic diversity of crocodyliforms, non-avian dinosaurs, and mammals known from the Campanian and Maastrichtian stages of South America, Africa, Antarctica, and the Indian subcontinent. The Campanian and Maastrichtian, the last two stages of the Late Cretaceous, represent a broader time slice (approximately 18.5 million years) than is likely represented by the Anembalemba Member of the Maevarano Formation in Madagascar. Nonetheless, the uneven comparison is necessitated, at least in part, because of the poor sampling of penecontemporaneous Gondwanan horizons and because of the imprecise dating of productive strata; given these constraints, it is better to be too inclusive rather than too exclusive. The faunal lists have been extracted from numerous sources for crocodyliforms (e.g., Gasparini et al., 1996; Bertini & Carvalho, 1999; Wilson et al., 2001; Prasad & de Lapparent de Broin, 2002), but primarily from Weishampel et al. (2004) for non-avian dinosaurs and Kielan-Jaworowska et al. (2004) for mammals, with other sources noted in table headings.

SOUTH AMERICA

South America has the largest and most diverse samples of Gondwanan Late Cretaceous vertebrates, many from Campanian and Maastrichtian horizons. Indeed, there are over 40 family-level taxa of terrestrial vertebrates known from the Campanian and Maastrichtian of South America, more than double the number from any other Gondwanan landmass. This is in large part the result of intense sampling over the past several decades, much of it owing to the efforts of José Bonaparte of the Museo Argentino de Ciencias Naturales Paleontologia (Buenos Aires) and his students.

It is not possible to determine which of the family-level taxa currently unknown from elsewhere were

Table 4. Crocodyliform genera from Campanian and Maastrichtian horizons in South America, Africa, Antarctica, and the Indian subcontinent. List for South America compiled primarily from Gasparini (1996) and Bertini and Carvalho (1999), for Africa from Buffetaut (1982) and Brochu (1997), and for the Indian subcontinent from Wilson et al. (2001) and Prasad and de Lapparent de Broin (2002).

South America
Mesoeucrocodylia
Metasuchia
Notosuchidae
Uruguaysuchus Rusconi
Baurusuchidae
Cynodontosuchus Woodward
Baurusuchus Price
Stratiotosuchus Campos, Suarez, Riff & Kellner
Peirosauridae
Peirosaurus Price
Lomasuchus Gasparini, Chiappe & Fernandez
Uberabasuchus Carvalho, Ribeiro & dos Santos Avilla
Trematochampsidae
Itasuchus Price
Metasuchia *incertae sedis*
Sphagesaurus Price
Neosuchia
Dyrosauridae
Sulcusuchus Gasparini & Spalletti
Hyposaurus Owen (questionably from Maastrichtian)
Eusuchia
Dolichochampsidae
Dolichochampsa Gasparini & Buffetaut
Africa
Mesoeucrocodylia
Neosuchia
Dyrosauridae
Sokotosuchus Halstead
Antarctica
No record
Indian Subcontinent
Mesoeucrocodylia
Metasuchia
Baurusuchidae
Pabwehshi Wilson, Malkani & Gingerich
Metasuchia *incertae sedis*
Genus indet.
Neosuchia
Dyrosauridae
Genus indet.

indeed restricted to South America and which were more broadly distributed in the Southern Hemisphere, simply because of the relative paucity of discoveries on other Gondwanan landmasses. However, it is significant to note that of the seven family-level taxa of crocodyliforms (Notosuchidae, Peirosauridae, Trematochampsidae), non-avian dinosaurs (Abelisauridae, Noasauridae, Saltasauridae (including Saltasaurinae)), and mammals (Sudamericidae) that have been identified as occurring in the Maastrichtian of Madagascar, *all* are known from the Campanian/Maastrichtian of South America. This is suggestive of close biogeographic ties and, indeed, a degree of cosmopolitanism that was unexpected before the MBP discoveries and that, moreover, is difficult to explain in the context of most recent paleogeographic reconstructions.

Crocodyliforms known from Campanian and Maastrichtian horizons in South America are diverse, comprising at least 12 named genera, most of them metasuchians. In addition to notosuchids, peirosaurids, and trematochampsids, the metasuchian family Baurusuchidae is represented. Neosuchians and eusuchians, for which definitive evidence has yet to be found in the Late Cretaceous of Madagascar, are also present in South America. The non-avian dinosaur fauna from the South American Campanian and Maastrichtian is dominated by saurischians. Among Theropoda, abelisauroid ceratosaurians (including both abelisaurids and noasaurids) are the most diverse and, among the Sauropoda, lithostrotians, including saltasaurines, dominate. Ornithischians are represented by spotty occurrences of ankylosaurs, euornithopods, and hadrosaurs. It is intriguing that, in contrast to the dominance of ornithischian herbivores in most Campanian terrestrial ecosystems on Laurasian-derived landmasses, ornithischians appear to be only minor components of Campanian ecosystems on most Gondwanan landmasses, if they are present at all (Currie, 1996). Campanian and Maastrichtian mammals from South America include a diversity of archaic nontribosphenic forms, including Austrotriconodontidae, Bondesiidae, Brandoniidae, Dryolestidae, Ferugliotheriidae, Mesungulatidae, Reigitheridae, and Sudamericidae. Of these, only the Sudamericidae is known to also occur in Madagascar (Krause et al., 1997b). In addition to this diversity of nontribosphenic taxa, there are two species of eutherians and questionable occurrences of "pediomyid" and peradectid marsupials.

Antarctica

Not unexpectedly, considering its ice-cover and harsh climate today, Antarctica has grudgingly yielded fossils of Late Cretaceous terrestrial vertebrates. They have been recovered from the Antarctic Peninsula (Vega and James Ross Islands) and include only specimens of dinosaurs (Hooker et al., 1991; Gasparini et al., 1996; Rich et al., 1999; Case et al., 2000, 2003). This appears to be largely the result of "bloat and float" taphonomic scenarios, where carcasses are washed out to sea and skeletal elements are buried in, and recovered from, marine sediments.

Table 5. Non-avian dinosaur genera from Campanian and Maastrichtian horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Weishampel et al. (2004), with additions from Novas and Agnolin (2004), Novas et al. (2004) for South America, Wilson and Upchurch (2003) for India, and Suberbiola et al. (2004) for Africa. Question marks indicate tentative placement.

SOUTH AMERICA
- Theropoda
  - Ceratosauria
    - Abelisauroidea
      - Abelisauridae
        - *Carnotaurus* Bonaparte
        - Abelisauridae indet.
      - Noasauridae
        - *Noasaurus* Bonaparte & Powell
  - Tetanurae
    - Avetheropoda
      - *Quilmesaurus* Coria
    - Maniraptora
      - *Unquillosaurus* Powell
    - ?Oviraptosauria indet.
    - Coelurosauria indet.
    - Theropoda indet.
- Sauropoda
  - Lithostrotia
    - Saltisauridae
      - *Saltasaurus* Bonaparte & Powell
  - Lithostrotia *incertae sedis*
    - *Aeolosaurus* Powell
    - *Antarctosaurus* Huene
    - *Laplatasaurus* Huene
    - *Neuquenosaurus* Powell
    - *Pelliginisaurus* Salgado
    - *Rocasaurus* Salgado & Azpilicueta
    - Lithostrotia indet.
  - Titanosauria indet.
  - Sauropoda indet.
- Thyreophora
  - Ankylosauria
    - ?Nodosauridae indet.
    - Ankylosauridae indet.
- Ornithopoda
  - Euornithopoda
    - Iguanodontia
      - *Talenkauen* Novas, Cambiaso & Ambrosio
    - Hadrosauridae
      - Hadrosaurinae indet.
      - Lambeosaurinae indet.
    - Euornithopoda indet.

AFRICA
- Theropoda
  - Ceratosauria
    - Abelisauroidea
      - ?Abelisauridae
        - Genus indet.
  - Avetheropoda *incertae sedis*
    - *Bahariasaurus* Stromer

Table 5. Continued.

- Sauropoda
  - Titanosauriformes indet.

ANTARCTICA
- Theropoda indet.
- Thyreophora
  - Ankylosauria
    - Nodosauridae indet.
- Ornithopoda
  - Euornithopoda
    - Hadrosauridae indet.

INDIAN SUBCONTINENT
- Theropoda
  - Ceratosauria
    - Abelisauroidea
      - Abelisauridae
        - *Indosaurus* Huene & Matley
        - *Indosuchus* Huene & Matley
        - *Rajasaurus* Wilson, Sereno, Srivastiva, Bhatt, Khosla & Sahni
        - Genus indet. A
        - Genus indet. B
      - Noasauridae
        - *Laevisuchus* Huene & Matley
    - Ceratosauria indet.
    - ?Carnosauria indet.
      - *Compsosuchus* Huene & Matley
    - Ornithomimidae indet.
    - Theropoda indet.
- Sauropoda
  - Lithostrotia
    - *Isisaurus* Wilson & Upchurch
    - *Jainosaurus* Hunt, Lockley, Lucas & Meyer
    - *Antarctosaurus*
  - Titanosauria indet.
  - Sauropoda indet.
- Thyreophora
  - Ankylosauria
    - Ankylosauridae indet.
  - Stegosauria
    - Stegosauridae indet.

This also may account for the lack of discovery of small vertebrate taxa (e.g., lizards, turtles, crocodyliforms, mammals), although climate may have also played an important role. Interestingly, the dinosaur fossils that have been recovered are of taxa (e.g., Euornithopoda, Hadrosauridae, Nodosauridae) that are not represented in the Campanian/Maastrichtian of Africa, Madagascar, or the Indian subcontinent. Instead they are shared with penecontemporaneous horizons in South America.

AFRICA

Africa is, by far, the largest Gondwanan landmass, roughly 70% larger than the next largest, South

Table 6. Mammalian genera from Campanian and Maastrichtian horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Kielan-Jaworowska et al. (2004), with additions from Rana and Wilson (2003) and Khosla et al. (2004) for the Indian subcontinent. Question marks indicate questionable occurrences and quotation marks indicate paraphyletic taxa.

South America
?Docodonta
  Reigitheriidae
    Reigitherium Bonaparte
Eutricondonta
  Austrotriconodontidae
    Austrotriconodon Bonaparte
?Multituberculata *incertae sedis*
    Genus indet.
Archaic "symmetrodontans"
  Bondesiidae
    Bondesius Bonaparte
Stem Cladotheria
  Dryolestidae
    Groebertherium Bonaparte
    Leonardus Bonaparte
    Genus indet.
  Mesungulatidae
    Mesungulatum Bonaparte & Soria
  Brandoniidae
    Brandonia Bonaparte
    ?*Casamiguelia* Bonaparte
Marsupialia
  ?Peradectidae
    Genus indet.
  ?"Pediomyidae"
    Genus indet.
Eutheria
  Family *incertae sedis*
    Perutherium Grambast, Martinez, Mattauer & Thaler
    Genus indet.
Gondwanatheria
  Sudamericidae
    Gondwanatherium Bonaparte
  Ferugliotheriidae
    Ferugliotherium Bonaparte
Africa*
No record
Antarctica
No record
Indian Subcontinent
Eutheria
  ?Otlestidae
    Genus indet.
  Family *incertae sedis*
    Deccanolestes Prasad & Sahni
    Sahnitherium Rana & Wilson
Infraclass *incertae sedis*
  Gondwanatheria
    Sudamericidae
      Genus indet.

* A possible gondwanatherian mammal was recently described by Krause et al. (2003b), but the age of the horizon from which it was recovered is of uncertain age within the Cretaceous period.

America. Despite its vast superiority in size among the five Gondwanan landmasses considered here, Africa's diversity of Campanian/Maastrichtian terrestrial vertebrates is the second poorest, little better than that from Antarctica. This is presumably due in large part to the virtual absence of suitable sedimentary depocenters of the right age and environment, but further exacerbated by limited exploration and a lack of definitive age control independent of the vertebrate fossils themselves.

Of the seven identified families of crocodyliforms, non-avian dinosaurs, and mammals represented in Madagascar, only one, Abelisauridae, is represented, albeit questionably, in the Campanian/Maastrichtian of Africa. Among crocodyliforms, Metasuchia, the crocodyliform clade that dominates in penecontemporaneous horizons in South America, Madagascar, and the Indian subcontinent, is absent. Instead, only the neosuchian dyrosaurid *Sokotosuchus* is known. Among non-avian dinosaurs, there is only poorly preserved material, none of which is precisely identified; significantly, however, no ornithischians are currently known. Campanian/Maastrichtian mammals have yet to be discovered from mainland Africa, although the possible gondwanatherian recently described by Krause et al. (2003b) could conceivably be from this horizon.

The Indian Subcontinent

The record of terrestrial vertebrates from the latest Cretaceous of the Indian subcontinent has increased dramatically over the last three decades, largely the result of efforts by Ashok Sahni of Panjab University (Chandigarh) and his students. The assemblage, from below and interbedded within the Deccan Traps (the infra- and intertrappean beds) was recently summarized by Khosla and Sahni (2003). The infra- and intertrappean beds are considered to be of late Maastrichtian age. The diversity of terrestrial vertebrates from the Indian subcontinent is low, and surprisingly low in one clade that is diverse elsewhere, the Crocodyliformes. Two metasuchians (Baurusuchidae and Metasuchia *incertae sedis*) and one neosuchian (Dyrosauridae) are present, but none of the metasuchian families identified in Madagascar (Notosuchidae, Peirosauridae, Trematochampsidae) have been definitively identified on the Indian

←

subcontinent. Non-avian dinosaurs were discovered on the Indian subcontinent over 175 years ago. Many specimens have been discovered since and demonstrate that a diverse fauna existed at this time. Unfortunately, however, few articulated specimens have been recovered and, as a result, the alpha taxonomy remains ambiguous. Nonetheless, it is clear that the most common dinosaurs present at this time in Madagascar (abelisaurid and noasaurid theropods and lithostrotian sauropods) were also present on the Indian subcontinent. The mammalian fauna is represented by fragmentary isolated teeth that have been assigned to at least three eutherian taxa (*Deccanolestes*, *Sahnitherium*, and a possible otlestid) and a sudamericid gondwanathere (Prasad & Sahni, 1988; Godinot & Prasad, 1994; Prasad & Godinot, 1994; Prasad et al., 1994; Krause et al., 1997b; Rana & Wilson, 2003; Khosla et al., 2004).

SUMMARY

It is clear, based on currently available samples, that the greatest similarity in taxonomic composition of known Campanian/Maastrichtian terrestrial vertebrate faunas to that of Madagascar occurs in South America and India.

Table 7. Crocodyliform genera from pre-Campanian Late Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. List for South America compiled primarily from Bertini and Carvalho (1999), and for Africa from Buffetaut (1982) and Larsson and Gado (2000).

SOUTH AMERICA
Mesoeucrocodylia
  Metasuchia
    Notosuchidae
      Notosuchus Woodward
      Mariliasuchus Carvalho & Bertini
      Comahuesuchus Bonaparte
AFRICA
Mesoeucrocodylia
  Metasuchia
    Libycosuchidae
      Libycosuchus Stromer
    Trematochampsidae
      Hamadasuchus Buffetaut
      Trematochampsa
  Eusuchia
    Stomatosuchidae
      Stomatosuchus Stromer
      Aegyptosuchus Stromer
ANTARCTICA
No record
INDIAN SUBCONTINENT
No record

PRE-CAMPANIAN CRETACEOUS DISTRIBUTION OF CROCODYLIFORMS, NON-AVIAN DINOSAURS, AND MAMMALS ON GONDWANAN LANDMASSES

In addition to comparing the taxonomic composition of crocodyliforms, non-avian dinosaurs, and mammals from Campanian/Maastrichtian horizons of Madagascar, South America, Africa, Antarctica, and the Indian subcontinent, it is relevant to record the pre-Campanian Cretaceous distributions of these same clades on these same landmasses in order to potentially reveal deeper histories. As such, Tables 7–9 provide an overview of the generic diversity of crocodyliforms, non-avian dinosaurs, and mammals from the pre-Campanian Late Cretaceous, whereas Tables 10–12 provide the same information for the Early Cretaceous. The pre-Campanian Late Cretaceous and Early Cretaceous distributions are listed individually because there is general agreement among paleogeographers and paleontologists that South America and Africa separated near the Early/Late Cretaceous boundary (see below). Each of the clades will be considered in turn.

CROCODYLIFORMS (TABLES 7, 10)

Notosuchids, but not trematochampsids, are known from the pre-Campanian Late Cretaceous of South America, whereas trematochampsids, but not notosuchids, are known from the pre-Campanian Late Cretaceous of Africa. Both notosuchids and trematochampsids, as well as the unplaced metasuchian *Araripesuchus*, are recorded from Early Cretaceous horizons in both South America and Africa. This reveals a deeper history on those landmasses, presumably prior to separation of these landmasses near the Early/Late Cretaceous boundary. Peirosaurids are known from the Early Cretaceous of Africa but not South America and from neither landmass during the pre-Campanian Late Cretaceous. Unfortunately, the record of identifiable pre-Campanian Cretaceous crocodyliforms is nonexistent for Antarctica and the Indian subcontinent.

NON-AVIAN DINOSAURS (TABLES 8, 11)

Pre-Campanian non-avian dinosaur faunas from Gondwana, particularly from Africa and South America, are generally much better characterized than their Campanian/Maastrichtian counterparts, in part owing to the higher incidence of basin formation (with concurrent sedimentation) during these times. Abelisaurids and lithostrotians are known from Africa and South America during both pre-Campanian Late

Table 8. Non-avian dinosaur genera from pre-Campanian Late Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Weishampel et al. (2004), with additions from González Riga (2003) and Apesteguía (2004) for South America and Sereno et al. (2004) for Africa. Question marks indicate tentative placement.

SOUTH AMERICA

- Theropoda
  - Ceratosauria
    - *Xenotarsosaurus* Martinez, Gimenez, Rodriguez & Bochatey
    - *Velocisaurus* Bonaparte
    - Abelisauroidea
      - Abelisauridae
        - *Abelisaurus* Bonaparte & Novas
        - *Aucasaurus* Coria, Chiappe & Dingus
        - *Ilokelesia* Coria & Salgado
      - Abelisauridae indet.
  - Tetanurae
    - ?Coelurosauria
      - *Aniksosaurus* Martinez & Novas
    - Avetheropoda
      - Allosauroidea
        - *Giganotosaurus* Coria & Salgado
      - Dromaeosauridae
        - *Unenlagia* Novas
        - *Megaraptor* Novas
    - Dromaeosauridae indet.
    - Troodontidae indet.
    - ?Ornithomimidae indet
    - Tetanurae indet
    - Theropoda indet.
- Sauropoda
  - Diplodocoidea
    - *Amazonsaurus* Carvalho, Avilla & Salgado
    - *Rayososaurus* Bonaparte
    - Titanosauria
      - *Andesaurus* Calvo & Bonaparte
      - *Argentinosaurus* Bonaparte & Coria
      - *Argyrosaurus* Lydekker
      - *Bonitasaura* Apesteguia
      - *Epacthosaurus* Powell
      - *Mendozasaurus* González Riga
      - Titanosauria indet.
    - Lithostrotia
      - *Antarctosaurus*
      - *Laplatasaurus*
      - *Rinconsaurus* Calvo & González Riga
      - Lithostrotia indet.
      - Saltasauridae
        - *Neuquensaurus* Powell
        - *Saltasaurus*
    - Sauropoda indet.
- Ornithopoda
  - Euornithopoda
    - *Notohypsilophodon* Martinez
    - Iguanodontia
      - *Anabisetia* Coria & Calvo
      - *Gasparinisaura* Coria & Salgado

Table 8. Continued.

- Hadrosauridae
  - *Secernosaurus* Brett-Surman
- ?Iguanodontia indet.
- Ornithopoda indet.

AFRICA

- Theropoda
  - Ceratosauria
    - Abelisauroidea
      - Abelisauridae
        - *Rugops* Sereno, Wilson & Conrad
        - Abelisauridae indet.
      - Noasauridae
        - *Deltadromeus* Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio & Wilson
  - Tetanurae
    - *Sigilmassasaurus* Russell
    - Spinosauroidea
      - Spinosauridae
        - *Spinosaurus* Stromer
    - Avetheropoda
      - Carcharodontosauridae
        - *Carcharodontosaurus* Stromer
    - Avetheropoda *incertae sedis*
      - *Bahariasaurus*
    - Dromaeosauridae indet.
    - Theropoda indet.
- Sauropoda
  - Diplodocoidea
    - Dicraeosauridae
      - cf. *Dicraeosaurus* Janensch
    - Titanosauria *incertae sedis*
      - *Aegyptosaurus* Stromer
    - Lithostrotia
      - *Paralititan* Smith, Lamanna, Lacovara, Dodson, Smith, Poole, Giegengack, Attia
    - Dicraeosauridae indet.
    - Lithostrotia indet.
    - Sauropoda indet.
- Ornithopoda
  - Euornithopoda
    - Iguanodontia
      - Hadrosauridae
        - cf. *Ouranosaurus* Taquet*
    - Euornithopoda indet.*
    - Iguanodontia indet.*
    - Ornithopoda indet.

ANTARCTICA

- Theropoda indet.

INDIAN SUBCONTINENT

- Theropoda
  - Theropoda indet.
- Sauropoda
  - Sauropoda indet. (= *Bruhathkayosaurus* Yadagiri & Ayyasami)
- Stegosauria
  - Stegosauridae
    - *Dravidosaurus* Yadagiri & Ayyasami

* Indicates taxa listed from only Marsa Matruh, Egypt (?Albian–Cenomanian)

Table 9. Mammalian genera from pre-Campanian Late Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Kielan-Jaworowska et al. (2004).

South America
Mammalia indet.
Africa
Mammalia indet.
Antarctica
No record
Indian Subcontinent
No record

Table 10. Crocodyliform genera from Early Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. List for South America compiled primarily from Bertini and Carvalho (1999), and for Africa from Buffetaut (1982) and Larsson and Gado (2000). Question mark indicates tentative placement.

South America
Mesoeucrocodylia
Metasuchia
Notosuchidae
Candidodon Carvalho & Campos
Trematochampsidae
Amargasuchus Chiappe
?Trematochampsidae
Caririsuchus Kellner
Metasuchia *incertae sedis*
Araripesuchus
Neosuchia
Pholidosauridae
Sarcosuchus Marsh
Meridiosaurus Mones
Africa
Mesoeucrocodylia
Metasuchia
Notosuchidae
Malawisuchus Jacobs, Winkler, Downs & Gomani
Anatosuchus Sereno, Sidor, Larsson & Gado
Peirosauridae
Stolokrosuchus Larsson & Gado
Trematochampsidae
Hamadasuchus
Libycosuchidae
Libycosuchus
Metasuchia *incertae sedis*
Araripesuchus
Neosuchia
Pholidosauridae
Sarcosuchus
Neosuchia *incertae sedis*
Brillanceausuchus Michard, de Broin, Brunet & Hell
Antarctica
No record
Indian Subcontinent
No record

Cretaceous and Early Cretaceous intervals, thereby indicating the initial diversification of these clades prior to the breakup of Gondwana. Noasaurids are also known from Africa during these same intervals, but their occurrence in South America is limited to the pre-Campanian Late Cretaceous. The phylogenetic ambiguity resulting from the relatively fragmentary skeletal material of many of these taxa, particularly noasaurids and lithostrotians, however, necessarily limits biogeographic inferences derived from them.

Similar to the situation described above for Campanian/Maastrichtian strata of non-Madagascan Gondwanan landmasses, pre-Campanian Cretaceous deposits, particularly of South America and Africa, also preserve diverse non-avian dinosaur faunas characterized by numerous clades of tetanuran theropods, non-lithostrotian sauropods, ornithopods, ankylosaurians, and stegosaurians. Particularly problematic for Gondwanan-wide biogeographic reconstructions is the virtual absence of Early Cretaceous dinosaur discoveries from Antarctica, India, and Madagascar.

MAMMALS (TABLES 9, 12)

None of the lower-level mammalian taxa recovered from the Maastrichtian of Madagascar are shared with pre-Campanian Cretaceous horizons from other Gondwanan landmasses, but the biogeographic relevance of this information is limited by the extremely poor knowledge of the mammalian fossil record for the entire Cretaceous of Gondwana. With the possible exceptions of a caudal vertebra from Libya (Nessov et al., 1998) and a dentary fragment from Brazil (Bertini et al., 1993), both of which were recovered from poorly age-constrained horizons (Santonian-Campanian), there are no known pre-Campanian Late Cretaceous mammals known from Gondwanan landmasses. In addition to an important assemblage from Australia, Early Cretaceous Gondwanan mammals are known only from Africa and South America. A Barremian site in Cameroon has yielded evidence of at least three nontribosphenic therians, only one of which, the peramurid "eupantotherian" *Abelodon*, has been named (Brunet et al., 1990). By contrast, a diverse mammalian fauna of Berriasian age has been recovered from Morocco and includes eutriconodontans, archaic "symmetrodontans," "eupantotherians," and "tribotherians" (Sigogneau-Russell et al., 1998). A late Hauterivian or early Barremian site in Argentina has yielded numerous skeletal remains of the zatherian *Vincelestes* (e.g., Hopson & Rougier, 1993), but this is the only South American mammal site of definitive Early Cretaceous age.

Table 11. Non-avian dinosaur genera from Early Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Weishampel et al. (2004) with additions from Leanza et al. (2004) for South America and Sereno et al. (2004) for Africa.

SOUTH AMERICA
- Theropoda
  - Ceratosauria
    - *Ligabueino* Bonaparte
  - Ceratosauria indet.
  - Abelisauridae indet.
  - Tetanurae
    - Spinosauroidea
      - Spinosauridae
        - *Irritator* Martill, Cruickshank, Frey, Small & Clarke
        - *Angaturama* Kellner & Campos
    - Avetheropoda
      - Allosauroidea
        - Carcharodontosauridae indet.
      - Tyrannosauroidea
        - *Santanaraptor* Kellner
    - Compsognathidae indet
    - Oviraptorosauria indet.
    - Theropoda indet.
- Sauropoda
  - Diplodocoidea
    - *Amargasaurus* Salgado & Bonaparte
    - *Rayososaurus*
    - Rebbachisauridae indet.
  - Titanosauria
    - *Agustinia* Bonaparte
    - *Chubutisaurus* del Corro
    - Titanosauria indet.
- Thyreophora
  - Stegosauridae indet.
- Ornithopoda
  - Euornithopoda
    - Iguanodontia indet.
- Ornithischia indet.

AFRICA
- Theropoda
  - Ceratosauria
    - *Spinostropheus* Sereno, Wilson & Conrad
    - Abelisauroidea
      - Noasauridae indet.
      - Abelisauridae indet.
  - Tetanurae
    - *Afrovenator* Sereno, Wilson, Larsson, Dutheil & Sues
    - Spinosauroidea
      - Spinosauridae
        - *Spinosaurus*
        - *Suchomimus* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadlier, Sidor, Varricchio, Wilson & Wilson
      - Spinosauridae indet.
    - Avetheropoda
      - Carcharodontosauridae

Table 11. Continued.

        - *Carcharodontosaurus* Stromer
    - Avetheropoda *incertae sedis*
      - *Bahariasurus* Stromer
    - Coelurosauria *incertae sedis*
      - *Nqwebasaurus* de Klerk, Forster, Sampson, Chinsamy & Ross
    - Tetanurae indet.
    - Theropoda indet.
- Sauropoda
  - Diplodocoidea
    - Rebbachisauridae
      - *Nigersaurus* Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadlier, Sidor, Varricchio, Wilson & Wilson
      - *Rebbachisaurus* Lavocat
    - Diplodocidae indet.
  - Macronaria
    - *Jobaria* Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadlier, Sidor, Varricchio, Wilson & Wilson
  - Titanosauriformes
    - *Brachiosaurus* Riggs
    - Lithostrotia
      - *Malawisaurus*
    - Lithostrotia indet.
    - Sauropoda indet.
- Thyreophora
  - Ankylosauria
    - Nodosauridae indet.
  - Stegosauria
    - *Paranthodon* Nopcsa
  - Thyreophora indet.
- Ornithopoda
  - Euornithopoda
    - Iguanodontia
      - *Lurdusaurus* Taquet & Russell
      - *Valdosaurus* Galton
      - Hadrosauridae
        - *Ouranosaurus*
    - Iguanodontia indet.
- Ornithischia indet.

ANTARCTICA
No record

INDIAN SUBCONTINENT
No record

MADAGASCAR
No record

SUMMARY

Current evidence suggests a number of close biogeographic ties linking pre-Campanian Cretaceous faunas from Africa and South America. However, it must be noted that data to evaluate faunal links with other Gondwanan landmasses, including Madagascar, are minimal. The undescribed faunal assemblage from the Ankazomihaboka sandstones (Curry, 1997; Curry et al., in prep) may have a significant bearing in this regard.

Table 12. Mammalian genera from Early Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. List compiled from Kielan-Jaworowska et al. (2004), with additions from Hahn and Hahn (2003). Question mark indicates tentative placement and quotation marks indicate paraphyletic taxa.

SOUTH AMERICA
"Eupantotheria"
Zatheria
Vincelestidae
Vincelestes Bonaparte
AFRICA
Mammalia
Family incertae sedis
Genus indet. A
Genus indet. B
Eutriconodonta
?"Amphilestidae"
Genus indet.
Family indet.
Dyskritodon Sigogneau-Russell
Ichthyoconodon Sigogneau-Russell
Multituberculata
Hahnodontidae
Denisodon Hahn & Hahn
Hahnodon Sigogneau-Russell
Genus indet.
Archaic "symmetrodontans"
Family indet.
Atlasodon Sigogneau-Russell
Microderson Sigogneau-Russell
Thereuodontidae
Thereuodon Sigogneau-Russell
Stem Cladotheria ("eupantotherians")
Family indet.
Genus indet.
Afriquiamus Sigogneau-Russell
Minimus Sigogneau-Russell
Donodontidae
Donodon Sigogneau-Russell
Peramuridae
Abelodon Brunet, Coppens, Dejax, Flynn, Heintz, Hell, Jacobs, Jehenne, Mouchelin, Pilbeam & Sudre
Peramus Owen
Stem Boreosphenida
Aegialodontidae
Hypomylos Sigogneau-Russell
Family indet.
Tribotherium Sigogneau-Russell
ANTARCTICA
No record
INDIAN SUBCONTINENT
No record

PHYLOGENY AND BIOGEOGRAPHY OF LATE CRETACEOUS CROCODYLIFORMS, NON-AVIAN DINOSAURS, AND MAMMALS FROM MADAGASCAR

Of the seven family-level taxa of crocodyliforms, non-avian dinosaurs, and mammals known from the Maastrichtian of Madagascar, all are shared with Campanian/Maastrichtian faunas of South America. This is suggestive of close biogeographic ties and, indeed, a degree of cosmopolitanism that is difficult to explain in the context of most recent paleogeographic reconstructions depicting separation of most Gondwanan landmasses by great distances at this time (e.g., Lawver et al., 1992; Smith et al., 1994; Reeves & de Wit, 2000; Marks & Tikku, 2001; Rotstein et al., 2001; Scotese, 2001; O'Neill et al., 2003; de Wit, 2003; Bernard et al., 2005). According to these reconstructions, Madagascar had long been isolated in the Indian Ocean by the Campanian and, more specifically, any terrestrial continuity with South America, by whatever route, had been severed some 50 million years earlier. However, the record of Late Cretaceous terrestrial vertebrates from Gondwana is spotty at best and therefore difficult to interpret in a biogeographic context. The best possibilities for obtaining a biogeographic signal come from crocodyliforms, non-avian dinosaurs, and mammals, in part because of their relatively good preservation and therefore relatively precise identification, and in part because they are relatively well-studied. Indeed, the recent publication of two monumental works, by Weishampel et al. (2004) on dinosaurs and Kielan-Jaworowska et al. (2004) on mammals, facilitates the compilation of occurrence data that are used herein to reveal distributional patterns for these taxa. Here we document the available taxonomic and phylogenetic information that might have a more immediate bearing on our understanding of Gondwanan biogeography.

CROCODYLIFORMS

Phylogenetic analyses have been presented for only three of the seven species of crocodyliforms known from the Late Cretaceous of Madagascar. The phylogenetic relationship of *Mahajangasuchus insignis* to other metasuchians was examined by Buckley and Brochu (1999) and Buckley et al. (2000). These analyses indicated a clade that consisted of *Trematochampsa* + *Mahajangasuchus* + Peirosauridae, with *Araripesuchus* basal to this clade. This result tends to support the contention of Buffetaut (1988, 1989), who argued that Peirosauridae should be considered a junior synonym of Trematochampsidae. Without more conclusive evidence and a more thorough understanding of trematochampsid taxa, *Mahajangasuchus* was classified as Metasuchia

incertae sedis. Tykoski et al. (2002) and Turner and Calvo (2005) obtained identical results to Buckley and Brochu (1999). Carvalho et al. (2004) did not include any traditional trematochampsids in their analysis, but found *Mahajangasuchus* to be embedded within the Peirosauridae, with *Uberabasuchus* Carvalho, Ribeiro & dos Santos Avilla from the Late Cretaceous of Brazil as its most closely related sister taxon.

Buckley et al. (2000) determined that *Simosuchus* and its closest sister taxon, *Uruguaysuchus*, from the Late Cretaceous of Uruguay, formed a clade with *Malawisuchus*, and that these three taxa were questionable members of the Notosuchidae (which included *Notosuchus* + *Libycosuchus* in their analysis). This relationship was supported by several subsequent analyses. Tykoski et al. (2002) recovered a nearly identical tree, with *Simosuchus* and *Uruguaysuchus* linked as closely related sister taxa within a notosuchian clade. Sereno et al. (2003) placed *Simosuchus* within the Notosuchia (including a *Comahuesuchus* + *Anatosuchus* clade and a *Simosuchus* + *Araripesuchus* + traditional sebecosuchians + *Malawisuchus* + *Notosuchus* clade). Tree topology regarding this clade is nearly identical with the earlier study by Buckley et al. (2000), with the exception of the exclusion of *Araripesuchus* from the Notosuchia. Sereno et al. (2003) additionally recognized an expanded concept of Notosuchia, roughly equivalent to the Ziphosuchia proposed by Ortega et al. (2000), by including *Comahuesuchus*, *Anatosuchus*, and *Baurusuchus* + *Sebecus* Simpson. Pol (2003) recovered a tree similar to those of Buckley et al. (2000) and Sereno et al. (2003), with *Simosuchus* firmly nested within Notosuchia. The constituency of his notosuchian clade strongly reflects that proposed by Ortega et al. (2000) and Sereno et al. (2003), with the only key difference being the exclusion of *Araripesuchus*, as was also proposed by Buckley et al. (2000). It is worth noting that Ortega et al. (2000) and Pol (2003) include several taxa not included in the other two analyses, resulting in a more geographically widespread notosuchian (or ziphosuchian) clade. These taxa include *Chimaerasuchus* Wu, Sues & Sun from the Early Cretaceous of China and *Iberosuchus* Antunes from the Paleogene of Europe. Turner and Calvo (2005) essentially mirrored the earlier results of Buckley et al. (2000) in producing a *Malawisuchus* + *Uruguaysuchus* + *Simosuchus* clade within the Notosuchia.

The most contrary hypothesis regarding the relationship of *Simosuchus* to other mesoeucrocodylians was put forth by Carvalho et al. (2004). They placed the genus, along with *Chimaerasuchus*, within the Chimaerasuchidae, a clade basal to their Notosuchimorpha. Other differences also appear in their results, including the exclusion of *Uruguaysuchus* from the Notosuchia and the placement of *Malawisuchus* within the Peirosauroidea. It is likely that these discrepancies are due to the authors' reweighting of characters based upon rescaled values, a practice not followed by other studies.

A recent biogeographic study by Turner (2004b) is highly relevant to the question of Cretaceous crocodyliform distribution. Turner (2004b), employing a time-slicing protocol adapted from Upchurch et al. (2002), conducted a cladistic biogeographic analysis of a diverse sample of Cretaceous crocodyliform taxa, mostly from Gondwana. Included in his sample were three taxa known from the Late Cretaceous of Madagascar: *Simosuchus clarki*, *Mahajangasuchus insignis*, and *Araripesuchus* sp. indet. The sister taxon of *Simosuchus* in Turner's analysis is the Late Cretaceous South American form *Uruguaysuchus*, thus supporting an earlier assessment by Buckley et al. (2000). Turner resolved a sister taxon relationship between *Mahajangasuchus* and the South American Peirosauridae, which also supports the earlier analyses of Buckley and Brochu (1999) and Buckley et al. (2000). *Araripesuchus* sp. indet. occurs at the base of a clade of other *Araripesuchus* species from both Africa and South America. In his analysis, Turner also included *Pabwehshi*, a ?Maastrichtian mesoeucrocodylian from the Indian subcontinent recently described by Wilson et al. (2001). Turner (2004b) confirmed inclusion of *Pabwehshi* in the Baurusuchidae, otherwise only known from the Late Cretaceous of Brazil and Argentina. Late Cretaceous crocodyliforms from the Indian subcontinent are poorly known, based almost exclusively on isolated teeth (Prasad & de Lapparent de Broin, 2002). However, based on available information, Malagasy and Indian crocodyliforms share closest affinities with roughly contemporaneous taxa from South America.

Turner (2004b) refined the methods of Upchurch et al. (2002) and revealed two continent-level vicariant events: (1) separation of Africa, South America, and Indo-Madagascar from other non-Gondwanan landmasses earlier in the Cretaceous, and (2) separation of Africa from South America and Indo-Madagascar later in the Cretaceous. Turner (2004b: 2007) states that "this later event depicts a rather non-traditional biogeographic relationship and, in that respect, this study's results are similar to and support the conclusions of Sampson et al. (1998), Buckley and Brochu (1999), Krause et al. (1999), Krause (2001), and the geological data of Hay et al. (1999)."

NON-AVIAN DINOSAURS

It could be argued that non-avian dinosaurs are perhaps better suited than crocodyliforms for revealing biogeographic pattern as it relates to subaerial

landmasses, because they were likely more closely tied to the terrestrial realm. Moreover, most taxa were very large, making it less likely that they would have been able to raft across great distances on floating mats of vegetation, as has been documented for smaller-bodied extant vertebrates (Censky et al., 1998). As for crocodyliforms, the majority of non-avian dinosaur taxa known from the Late Cretaceous of Madagascar share closest affinities with penecontemporaneous taxa from South America and India. Preliminary phylogenetic analyses have been presented for all four of the saurischian taxa known from Madagascar (Sampson et al., 1998, 2001; Curry Rogers & Forster, 2001, 2004; Curry Rogers, 2002, 2005; Carrano et al., 2002).

Majungatholus, an abelisaurid, has been included in several recent phylogenetic analyses. Sampson et al. (1998) placed this Malagasy abelisaurid in a polytomy with *Indosaurus* and *Indosuchus* from the Maastrichtian of India, *Abelisaurus* from the Santonian of Argentina, and *Carnotaurus* from the Campanian-Maastrichtian of Argentina. Relationships within this polytomy were somewhat better resolved by Sampson et al. (2001) and Carrano et al. (2002), who posited that *Majungatholus* and *Carnotaurus* were sister taxa and that they, together, were the sister taxon of *Abelisaurus* (*Indosaurus* and *Indosuchus* were not included in the analyses). These results were in essence supported in a more comprehensive analysis by Tykoski and Rowe (2004). Coria et al. (2002) grouped *Majungatholus* with *Abelisaurus* and *Ilokelesia* in a polytomy that comprised the sister taxon of *Aucasaurus* + *Carnotaurus*. Wilson et al. (2003) described a new abelisaurid, *Rajasaurus*, from the Maastrichtian of India and reported results of another cladistic analysis of abelisaurids (later presented by Sereno et al., 2004), which concluded that *Abelisaurus*, *Rajasaurus*, and *Majungatholus* + *Carnotaurus* occupied successive nodes on a tree. The later study by Sereno et al. (2004) also included a newly named Cenomanian abelisaurid from Africa, *Rugops* (referred to as "Niger taxon 2" in Wilson et al., 2003). Most significantly, despite the shuffling positions among abelisaurid genera, all analyses have concluded that the closest known relatives of *Majungatholus* lie in Campanian-Maastrichtian horizons of Argentina and India.

Masiakasaurus is currently considered to be a noasaurid abelisauroid (Carrano et al., 2004; Sereno et al., 2004; Tykoski & Rowe, 2004). An analysis by Sereno et al. (2004) concluded that *Masiakasaurus* lies in an unresolved polytomy with *Noasaurus* from the ?late Campanian-Maastrichtian of Argentina, an unnamed genus from the Aptian-Albian of Niger, and *Deltadromeus* (originally regarded as a basal coelurosaurian by Sereno et al., 1996) from the Cenomanian of Morocco. When originally described by Sampson et al. (2001) and Carrano et al. (2002), the relationships of *Masiakasaurus* were also unresolved, although it was recognized that its affinities lay most closely with *Noasaurus*, *Laevisuchus*, *Genusaurus* Accarie, Beaudoin, Dejax, Fries, Michard & Taquet, and *Ilokelesia*, and secondarily with the abelisaurids *Majungatholus*, *Carnotaurus*, *Xenotarsosaurus*, and *Abelisaurus*. Additional remains of *Masiakasaurus* recovered during the 2003 field season are currently under study by M. Carrano, S. Sampson, and M. Loewen. In a preliminary report, Carrano et al. (2004: 44A) regard the Noasauridae to be abelisauroids "from the Cretaceous of Argentina (*Noasaurus*, *Velocisaurus*), India (*Laevisuchus*), Madagascar (*Masiakasaurus*), and possibly Europe and Africa."

Rapetosaurus has been included in several phylogenetic analyses, the most comprehensive by Curry Rogers (2005), but also by Curry Rogers and Forster (2001) and Wilson (2002). All three of these analyses agree in their resolution of a close relationship between *Nemegtosaurus* Nowinski from the Campanian-Maastrichtian of Mongolia and *Rapetosaurus*, but postulate different successive outgroups and close relatives. Curry Rogers and Forster (2001) and Curry Rogers (2005) identify a clade that includes *Malawisaurus* from the Aptian of Malawi and several taxa from India and/or South America (e.g., *Antarctosaurus*, *Agustinia*). Wilson (2002) instead identifies *Malawisaurus* as a more basal lithostrotian, with *Rapetosaurus* as the sister taxon to a clade of more derived titanosaurs including *Isisaurus colberti* Jain & Bandyopadhyay (from the Campanian-Maastrichtian of India) and Saltasauridae (including taxa from North America, Mongolia, and South America).

Malagasy Taxon B has recently been included in a more comprehensive analysis of titanosaur phylogeny (including over 29 purported titanosaurians; Curry Rogers, 2001, 2005); the strict consensus tree clearly resolves it as nested within the Saltasaurinae (sensu Wilson & Upchurch, 2003). Saltasaurines traditionally include only three South American genera (*Saltasaurus*, *Neuquensaurus*, and *Rocasaurus*) and are uniquely characterized by the presence of strongly procoelous, dorsoventrally compressed distal caudal vertebrae.

MAMMALS

Most of the mammalian taxa from the Late Cretaceous of Madagascar provide little biogeographic information, either because the specimens are too fragmentary to permit identification to a lower taxonomic level, or because the taxa represented are unknown from any other landmass. Such is clearly the

case for one isolated tooth of a large taxon and for a nearly complete skeleton (Krause, 2003a); both taxa, if they are different, cannot be identified as yet beyond Mammalia incertae sedis.

The presence of gondwanatheres, however, is important. The two teeth questionably identified as gondwanatherian are relatively uninformative, but the two specimens that have been assigned to *Lavanify miolaka*, a sudamericid, provide important biogeographic data. Sudamericids are elsewhere known from the Late Cretaceous and Paleocene of Argentina, the Late Cretaceous (Maastrichtian) of India, and the Eocene of Antarctica. *Lavanify* appears to be most closely related to the unnamed sudamericid from India (Krause et al., 1997b).

Paleogeographic Reconstructions: Were South America and Madagascar Connected in the Late Cretaceous?

Despite Madagascar's current position in the Eastern Hemisphere and South America's location in the Western Hemisphere, and despite differing details in depictions of Gondwanan paleogeography, it is clear that the two landmasses were much closer to one another in the Mesozoic than they are today. Prior to the break-up of Pangea, a non-obstructed (by oceanic waters) overland route across Africa spanning some 3000 km separated the two areas of interest; today the straight-line distance between South America and Madagascar is almost 8000 km. With the fragmentation of Gondwana, which is generally agreed to have commenced in earnest in the Late Triassic to Early Jurassic (Lawver et al., 1992; Torsvik et al., 2001; de Wit, 2003; Wells, 2003), Madagascar, as part of "East Gondwana" (also including the Indian subcontinent, Antarctica, and Australia), began to separate from "West Gondwana" (South America and Africa).

Initial rifting between the Indo-Madagascar block and Africa began during the Permo-Triassic, and seafloor spreading between the conjugate-rifted margins of southern Somalia, Kenya, and Tanzania (Western Somali Basin) and northern Madagascar commenced by the late Middle Jurassic (Lawver et al., 1992; Wells, 2003). By the Late Jurassic (approximately 160 Ma), a narrow seaway separated the east coast of Africa from Madagascar and the rest of the East Gondwana block. During the Late Jurassic, Indo-Madagascar shifted southward along the Davie Fracture Zone, ultimately coming to rest some 400 km off the east coast of Mozambique in the Early Cretaceous (130–120 Ma).

At about this same time (mid Early Cretaceous), seafloor spreading commenced between the Indo-Madagascar block and Antarctica-Australia (Lawver et al., 1992). Most workers (e.g., Lawver et al., 1992; Müller et al., 1993; Roeser et al., 1996; Marks & Tikku, 2001; Coffin et al., 2002; Kent et al., 2002; O'Neill et al., 2003) posit that a through-going seaway intervened between Indo-Madagascar and Antarctica-Australia by the mid to late Early Cretaceous (130–110 Ma) and that subsequent spreading between these landmasses proceeded rapidly. Several recent paleogeographic reconstructions, for instance, illustrate a separation between Antarctica and Indo-Madagascar of approximately 950–1100 km (employing 111 km/degree of latitude conversion) by 96 Ma and 1700–1850 km by 83 Ma (Rotstein et al., 2001: fig. 9; Bernard et al., 2005: figs. 4, 5; Schettino & Scotese, 2005: figs. 4, 33). In part to reconcile the developing record of vertebrate fossils, Hay et al. (1999) boldly proposed an "alternative global Cretaceous paleogeography" in which intermittent land connections persisted between Indo-Madagascar and Antarctica, across the Kerguelen Plateau, well into the Late Cretaceous (perhaps as late as 80 Ma). Case (2002) also proposed a persistent land bridge, although farther west, across the Gunnerus Ridge and Kainan Maru Seamount.

Finally, in the mid Late Cretaceous, another major rifting event linked to the Marion hotspot led to the separation of Madagascar and India. This episode of seafloor spreading was accompanied by an outpouring of flood basalts on both landmasses. Dates from these basalts cluster in age from approximately 91 to 84 Ma (Storey et al., 1995, 1997; Torsvik et al., 1998, 2001). With this final episode of Late Cretaceous rifting, the Indian subcontinent moved rapidly northeastward toward Eurasia (Randrianasolo et al., 1981; Storetvedt et al., 1992; Storey et al., 1995, 1997), and Madagascar, situated several hundred kilometers from mainland Africa across the Mozambique Channel, has remained isolated in the Indian Ocean ever since.

Rifting in "West Gondwana" between South America and Africa commenced in the Early Cretaceous, and by approximately 120 Ma an arm of the South Atlantic extended well northward between the two landmasses (Lawver et al., 1992; Müller et al., 1993; Smith et al., 1994; Scotese, 1998; Hay et al., 1999). Geophysical data indicate that a through-going seaway intervened between South America and Africa by the beginning of the Late Cretaceous (Nürnberg & Müller, 1991; Lawver et al., 1992, Müller et al., 1993; Pletsch et al., 2001), and normal marine communications, as evidenced by the distribution of Cretaceous echinoids and fishes (Maisey, 2000; Néraudeau & Mathey, 2000), were apparently established between the Western Tethys and the Southern Ocean domain by approximately 100 Ma. The Antarctic Peninsula and South Orkney group remained contiguous with the

southern tip of South America throughout the Late Cretaceous and well into the Tertiary (Lawver et al., 1992; Woodburne & Case, 1996; Hay et al., 1999; Reguero et al., 2002; Lawver & Gahagan, 2003).

There remains strong indication that Africa was the first major landmass to become isolated by circum-continental seaways during the breakup of Gondwana, with both geophysical and biogeographic data suggestive of isolation before the end of the Early Cretaceous (approximately 100 Ma). Whether or not Indo-Madagascar maintained intermittent connections with Antarctica via the Kerguelan Plateau (Hay et al., 1999) and/or the Gunnerus Ridge (Case, 2002) into the later stages of the Late Cretaceous remains debatable. Faunal data described in this report are, however, consistent with a scenario of faunal interchange among "East Gondwana" landmasses (Madagascar-Indian subcontinent-Antarctica) and South America until late in the Late Cretaceous (see below).

Gondwanan Fragmentation and Late Cretaceous Biogeography

Fragmentation of the Gondwanan supercontinent and dispersion of its constituent landmasses during the latter half of the Mesozoic Era undoubtedly had profound effects on resident faunas of terrestrial vertebrates and their subsequent evolutionary histories. Combining geophysical and stratigraphic data for Gondwanan breakup with observations of faunal distributions provides an unprecedented opportunity to reveal large-scale biogeographic patterns. However, invoking *ceteris parabis*, there is no reason to assume that geologic data, by their very nature, hold priority over paleontologic data or vice versa—yet all things are rarely equal. Unfortunately, for the Cretaceous of Gondwana, seldom are both the geologic and paleontologic data sufficient for specified temporal slices and geographic areas. For some times and places, the geologic data supporting paleogeographic reconstructions are sound, plentiful, and derived from independent sources, and resulting interpretations have been made with confidence. For other times and places, the fossils are numerous, well preserved, and have been incorporated into rigorous phylogenetic frameworks. In this regard, the developing Cretaceous record of terrestrial vertebrates from Gondwanan landmasses is beginning to provide an opportunity to further clarify the timing and sequence of Gondwanan fragmentation.

Tables 4–12 reveal a number of notable patterns in the distribution of Cretaceous Gondwanan terrestrial vertebrates. The same family-level taxa of crocodyliforms, non-avian dinosaurs, and mammals that were shared among Madagascar, the Indian subcontinent, and South America during Campanian/Maastrichtian times are not known from penecontemporaneous horizons in mainland Africa or, for that matter, Antarctica. Nonetheless, despite the intensity of recent exploration and collecting, the fossil record is not fully up to the task of testing whether or not this pattern is real, a point made repeatedly by our working group and others (e.g., Krause et al., 1997b, 1999; Forster, 1999; Rogers et al., 2000; Carrano et al., 2002; Lamanna et al., 2002; Krause, 2003b; O'Connor et al., 2006). The geologic stages of the Cretaceous for which the records of terrestrial fossil vertebrates from Madagascar, the Indian subcontinent, and South America are reasonably well sampled are, for the most part, the very stages for which the African record is poor, and vice versa. As emphasized by Krause et al. (1999: 6), "one of the key stumbling blocks ... is the virtual lack of terrestrial and freshwater vertebrates from the post-Cenomanian Late Cretaceous of Africa." The fossil record of terrestrial vertebrates from mainland Africa is much better for the Early Cretaceous and pre-Campanian Late Cretaceous than it is for the later stages of the Late Cretaceous, whereas the reverse is true for the other three landmasses, particularly Madagascar and the Indian subcontinent. To further complicate matters, the record of terrestrial vertebrate fossils from the Cretaceous of Antarctica remains all but nonexistent.

This uneven temporal sampling has inhibited, and still inhibits, definitive testing of two competing biogeographic hypotheses (Fig. 8). The first, recently formulated and labeled the "pan-Gondwana" hypothesis by Sereno et al. (2004), stipulates that various clades of terrestrial vertebrates were broadly distributed throughout Gondwana during the Early Cretaceous and that the much more limited distributions in the post-Cenomanian Late Cretaceous (including in Africa) are the result of poor sampling and/or differential extinction. A corollary of this hypothesis states that land connections between (1) Africa and South America, (2) South America and Antarctica, and (3) Antarctica and Indo-Madagascar were all severed "during a relatively brief interval at the beginning of the Late Cretaceous (ca. 100–90 Myr ago)" (Sereno et al., 2004: 1328). Implicit in this hypothesis, therefore, is the prediction that terrestrial vertebrate faunas on each of these major landmasses would become increasingly endemic during the Late Cretaceous, beginning at approximately 90 Ma. The second hypothesis, formulated by our working group (e.g., Krause et al., 1997b, 1999; Sampson et al., 1998, 2001) and recently dubbed the "Africa-first" hypothesis by Sereno et al. (2004), posits cosmopolitanism of Late Cretaceous terrestrial Gondwanan

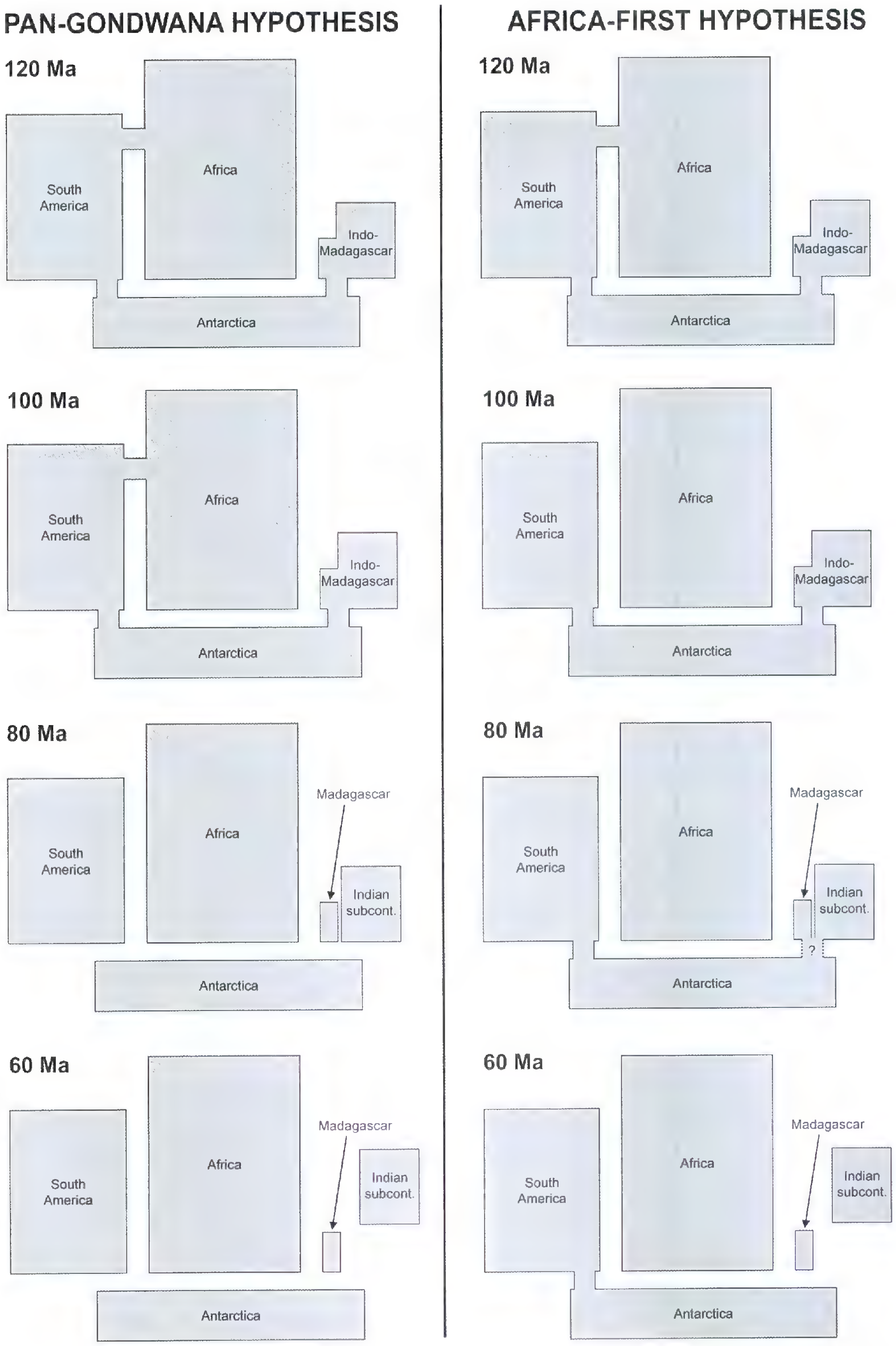

Figure 8. Schematic paleogeographic maps of major Gondwanan landmasses exclusive of Australia and southern Europe at 120, 100, 80, and 60 Ma depicting the major differences in purported land connections between the pan-Gondwana hypothesis (left column) and the Africa-first hypothesis (right column). The pan-Gondwana hypothesis posits separation of South America from Africa, South America from Antarctica, and Antarctica from Indo-Madagascar in a narrow time interval 100–90 Ma. The Africa-first hypothesis posits separation of South America from Africa before the beginning of the Late Cretaceous, South America from Antarctica in the Eocene, and Antarctica from Indo-Madagascar late in the Late Cretaceous.

faunas exclusive of Africa. More specifically, the latter model, generally consistent with the paleogeographic reconstruction of Hay et al. (1999), invoked Antarctica (in combination with two key land bridges) as a dispersal route between Indo-Madagascar (the Indian subcontinent plus Madagascar) and South America following isolation of Africa by a circum-African seaway prior to the beginning of the Late Cretaceous. According to this model, terrestrial vertebrate faunas on Africa are predicted to have become progressively more provincial during the Late Cretaceous (after separation between South America and Africa prior to the end of the Early Cretaceous), while those on other Gondwanan landmasses remained relatively cosmopolitan until considerably later in the period.

Sereno et al. (2004; see also Mahler, 2005) recently reported the important discovery of a number of definitive abelisauroid theropods (abelisaurids and noasaurids) in Aptian-Albian strata of Niger (approximately 110 Ma) and Cenomanian deposits of both Niger and Morocco (approximately 95 Ma), thus providing the first conclusive evidence for the presence of this clade in Africa. These finds support the pre-Late Cretaceous origin of Abelisauroidea on Gondwana, as previously indicated by several earlier discoveries in Argentina (Coria & Salgado, 1998; Lamanna et al., 2002; Rauhut et al., 2003). Thus, one alternative hypothesis of Sampson et al. (1998: 1050)—that "abelisaurids originated sometime in the Early Cretaceous after the tectonic isolation of Africa"—is clearly refuted. Based primarily on the new African abelisauroids, Sereno et al. (2004) concluded that the evidence therefore supports the pan-Gondwana hypothesis. We disagree with the latter contention, and regard the Africa-first hypothesis to be more consistent with the available, although admittedly limited, evidence (see below).

Before assessing this issue, it is necessary to address several statements by Sereno et al. (2004). First, these authors claimed that the original formulation of the Africa-first hypothesis by Sampson et al. (1998) included the stipulation that Africa and South America were fully separated by 140–120 Ma. Specifically, Sereno et al. (2004: 1328) stated that the Africa-first model, as portrayed by Sampson et al. (1998), "shows a circum-African seaway in the Early Cretaceous (ca. 140–120 Myr ago) that isolated the continent from other Gondwanan landmasses." Whereas Sampson et al. (1998: 1050) did state that "South America separated from Africa before 100 Ma" and, in the caption for Figure 4, specified "circa 120 Ma," claims for separation as early as 140 Ma were not made in that paper, or in any other paper published by our working group. Indeed, all of the paleogeographic reconstructions presented by us consistently show Africa and South America still joined at 120 Ma (Krause et al., 1997b: fig. 1, 1999: fig. 6; Sampson et al., 1998: fig. 4; Krause, 2003a: fig. 2.17; we specifically did not use the 120 million year reconstruction in Hay et al. (1999: figs. 12, 15), which illustrates full separation between South America and Africa at this time, but instead employed a reconstruction generated from the website operated by the Hay et al. working group (<http://www.odsn.de/odsn/services/paleomap/paleomap.html>), which shows these landmasses still connected by a narrow subaerial passage at 120 Ma). In any case, the portrayal by Sereno et al. (2004) of our Africa-first hypothesis as requiring isolation of Africa as early as 140 Ma is incorrect.

Second, Sereno et al. (2004: 1328–1329) concluded that "a permanent equatorial seaway of significant depth between South America and Africa was in place no earlier than the end of the Albian," and that "trans-Atlantic interchange may have been operative as late as 95 Myr ago." Elsewhere in the same paper, Sereno et al. (2004: 1328) stated that "well-constrained geological evidence (Reyment & Dingle, 1987; Pitman et al., 1993; Maisey, 2000) pinpoints the final separation of South America and Africa in the latest Albian (ca. 100 Myr ago), significantly later than proposed by the "Africa-first" model (ca. 140–120 Myr ago)." To clarify, the three papers cited by Sereno et al. do not make such definitive assessments. Reyment and Dingle (1987: 99) stated that "final continental separation was *probably* completed in Late [not latest] Albian time" (emphasis and bracketed words added), Pitman et al. (1993: 23) stated that "the point in time of final separation must be between 84 Ma … and 106 Ma," and Maisey (2000: 285) concluded that a permanent equatorial seaway joining the South Atlantic and the western Tethys Ocean had developed by the late Aptian (which ends at approximately 112 Ma; Gradstein et al., 2004). That said, it should be pointed out that there is other well-constrained geological evidence (Nürnberg & Müller, 1991; Pletsch et al., 2001) for a permanent marine connection between the central and southern parts of the Atlantic Ocean, separating South America from Africa by the late Aptian-early Albian, approximately 118–106 Ma (Gradstein et al., 2004). Again, we have never argued for separation of Africa and South America as early as 140 Ma, but it must be noted that current geophysical and paleogeographic evidence is suggestive of separation before the end of the Albian. As such, the primary distinction concerning this point is that Sereno's formulation of the pan-Gondwana hypothesis views separation between South America and Africa as having occurred *after* the end of the

Early Cretaceous, whereas the Africa-first hypothesis supports separation *before* the end of the Early Cretaceous.

Third, Sereno et al. (2004: 1328) made the claim that "other faunal evidence (notosuchian crocodylomorphs (Buckley et al., 2000) and gondwanatherian mammals (Sampson et al., 1998)) no longer supports the "Africa-first" model." While we agree that this evidence is far from strong or highly resolved, Sereno et al.'s conclusion simply does not follow from their explanatory statement that "African crocodylomorphs of mid-Cretaceous age (Aptian-Albian) are most closely related to taxa of comparable age on South America (Buffetaut & Taquet 1977, 1979; Sereno et al., 2003), and the absence of gondwanatheres reflects only the non-existent record of mammals on Africa during most of the Cretaceous." Close relationships among African and South American crocodylomorphs of Aptian-Albian age, which we do not dispute, cannot serve as evidence for no longer supporting the hypothesis that Africa was the first major Gondwanan landmass to become isolated. Furthermore, the recent cladistic biogeographic analysis by Turner (2004b), reviewed above, demonstrated that crocodyliform evidence is indeed consistent with the Africa-first hypothesis. Finally, the presence of sudamericid gondwanatheres in the Campanian/Maastrichtian of South America, Madagascar, and India was primarily used to support the hypothesis that this enigmatic clade of mammals was much more cosmopolitan in its distribution in the latest Cretaceous than previously realized (Krause et al., 1997b). The absence of sudamericid gondwanatheres from the Cretaceous of mainland Africa (which, in fact, may not be the case—see Krause et al., 2003b) is no less supportive of an Africa-first hypothesis than it was when the paper by Krause et al. (1997b) was published.

In light of the discussion above, let us reexamine the current evidence and assess the claims and implications of the competing biogeographic hypotheses by focusing on established geologic and biologic constraints. First, the pan-Gondwana hypothesis, as defined by Sereno et al. (2004), posits the existence of three narrow, intermittent land bridges, all severed in the early Late Cretaceous, approximately 100–90 Ma: one between Africa and South America, another between South America and Antarctica, and a third between Antarctica and Indo-Madagascar. Geologic evidence in support of this model was based on the paleocoastline maps of Scotese (2001). In contrast, a revised Africa-first model, incorporating recent data on African abelisauroids from the Albian and Cenomanian, postulates the separation of South America and Africa prior to the Early/Late Cretaceous boundary, but the persistence of land bridges that permitted faunal exchange through Antarctica between South America to the west and Indo-Madagascar to the east until well into the Late Cretaceous. According to this view, early stocks of abelisaurids (and other vertebrates) were present on at least South America and Africa (and perhaps other Gondwanan landmasses) by the late Early Cretaceous. Rifting of South America and Africa toward the end of the Early Cretaceous isolated at least two stocks of abelisaurids, one on each continent. Currently, there is no reason to assume that they had spread into Gondwanan landmasses outside of Africa and South America at that early stage, although this scenario is not inconsistent with available evidence. Similarly, in the absence of fossil evidence, we cannot yet know what happened to the isolated stock of abelisaurids on Africa during the Late Cretaceous. However, on the rest of Gondwana, a basal stock of Cenomanian abelisaurids (of which there is evidence in Argentina; Lamanna et al., 2002) diversified into closely related forms observed later in the Cretaceous in Argentina, Madagascar, and the Indian subcontinent. Lacking fossil evidence, this hypothesis does not stipulate when during the Late Cretaceous those basal stocks (or their descendants) first arrived on Madagascar and the Indian subcontinent; that is, they may have been present at the time South America and Africa separated or they may have dispersed much later from South America. However, this view is consistent with *all* phylogenetic evidence presented to date (Sampson et al., 1998; Carrano et al., 2002; Coria et al., 2002; Wilson et al., 2003; Sereno et al., 2004) and posits that the derived abelisaurids (including several horned forms) present in the Maastrichtian of India and Madagascar on the one hand, and the Campanian-Maastrichtian of South America on the other, shared a more recent common ancestor than either did with abelisaurids from Africa.

Concerning paleogeographic reconstructions, none, including Scotese (2001), depicted a situation in which all three land bridges were severed at approximately the same time in the early Late Cretaceous, approximately 100–90 Ma. As reviewed above, current evidence suggests that the South America/Africa land bridge ceased to exist prior to the Albian/Cenomanian boundary (i.e., prior to 100 Ma). Indeed, even Scotese (2001) depicted the two continents to be already well separated by 94 Ma (Schettino & Scotese (2000) show separation at 100 Ma). Current geologic evidence is most consistent with the separation of Africa and South America (and thus the isolation of Africa) by 100 Ma (Lawver et al., 1992; Smith et al., 1994; Marks & Tikku, 2001; Scotese, 2001; Kent et al., 2002). By contrast, a land

bridge between South America and Antarctica is thought to have been present throughout the Late Cretaceous and until at least the early Eocene (Lawver et al., 1992; Woodburne & Case, 1996; Hay et al., 1999; Reguero et al., 2002; Lawver & Gahagan, 2003); there is no evidence for a termination of connection 100–90 Ma. Finally, as detailed above, the timing of separation of Antarctica from Indo-Madagascar is controversial. Most reconstructions indicate that Indo-Madagascar became isolated from all other Gondwanan landmasses about 120 Ma, some 50 million years prior to the time that the Maevarano vertebrate assemblage (as well as those from India) was deposited (e.g., Lawver et al., 1992; Smith et al., 1994; Marks & Tikku, 2001; Rotstein et al., 2001; Scotese, 2001; Kent et al., 2002; Bernard et al., 2005). Notably, and in stark contrast, however, the tectonic modeling of Hay et al. (1999) provides support for the scenario posited by the Africa-first hypothesis in that a land bridge between Antarctica and Indo-Madagascar was maintained until approximately 80 Ma (cf. Case, 2002). In neither case is there evidence to indicate synchroneity with the separation of South America from either Africa or Antarctica at 100–90 Ma, as postulated by Sereno et al.'s (2004) pan-Gondwana model.

Concerning faunal evidence, the crocodyliforms, nonavian dinosaurs, and mammals recovered from the Maevarano Formation of northwestern Madagascar are taxonomically most similar to those known from Campanian/Maastrichtian horizons of South America and the Indian subcontinent (Krause et al., 1997b; Buckley & Brochu, 1999; Buckley et al., 2000; Krause, 2001; Wilson et al., 2001; Curry Rogers, 2002; Prasad & de Lapparent de Broin, 2002; Turner, 2004b). Because strength of biogeographic signal is proportional to the number of phylogenetically independent groups possessing the same congruent pattern of area cladograms, it is significant to note that the patterns of similarity are repeated among a growing number of phylogenetically independent groups (e.g., notosuchids, peirosaurids, trematochampsids, and the unclassified metasuchian genus *Araripesuchus* among crocodyliforms; abelisaurids, noasaurids, and saltasaurines among nonavian dinosaurs; and sudamericids among mammals). This provides evidence for a high degree of cosmopolitanism among latest Cretaceous Gondwanan faunas outside of Africa that was not fully appreciated prior to recovery of the Maevarano assemblage and is unpredicted based on most recent paleogeographic reconstructions of the southern supercontinent (e.g., Lawver et al., 1992; Smith et al., 1994; Scotese, 1998, 2001; Marks & Tikku, 2001; Rotstein et al., 2001; Kent et al., 2002; Bernard et al., 2005; Schettino & Scotese, 2005) or the pan-Gondwanan hypothesis of Sereno et al. (2004).

Finally, the mere presence of abelisaurids and noasaurids on Africa 25 or more million years prior to their occurrence in Madagascar and India does not constitute evidence refuting the Africa-first hypothesis. Although recent discoveries demonstrate the presence of abelisauroids in the Early Cretaceous and earliest Late Cretaceous of mainland Africa, certainly an interesting and significant finding, phylogenetic analysis does not include placement of the recovered forms among the more derived members of this clade (Sereno et al., 2004). Indeed, the abelisaurid *Rugops* is postulated by Sereno et al. (2004) as the basalmost member of the group. Thus, although it appears that Africa did not separate from South America until near the Early/Late Cretaceous boundary, the closest relatives of *Majungatholus* and *Masiakasaurus* from the Maastrichtian of Madagascar are still found in Campanian/Maastrichtian horizons of South America and India. As such, there exists no faunal evidence to refute the hypothesis that Africa was the first among major Gondwanan landmasses to be fully isolated and, perhaps most importantly, that the terrestrial vertebrates of Gondwanan faunas outside of Africa were shared until late in the Late Cretaceous.

In summary, we regard the growing weight of latest Cretaceous biogeographic data as evidence in support of a modified Africa-first hypothesis. The close relationships of terrestrial vertebrates that lived on the Indian subcontinent and Madagascar near the end of the Cretaceous to penecontemporaneous taxa in South America appear incompatible with any proposed lengthy separation of Indo-Madagascar and South America prior to the Maastrichtian, whether that duration was approximately 50 million years, as indicated by most recent paleogeographic reconstructions of Cretaceous Gondwana, or approximately 25 million years, as posited by the pan-Gondwana hypothesis.

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EVOLUTION AND GEOGRAPHY: THE BIOGEOGRAPHIC HISTORY OF SOUTH AMERICAN LAND MAMMALS[1]

Rosendo Pascual[2]

Abstract

Based on the unequaled southern Late Cretaceous–Cenozoic record, the history of South American land mammals is divisible into two major episodes we term the Gondwanan Episode and the South American Episode. The former episode is distinguished by the northern and central Patagonian Argentinian record, while the latter is mostly based on the extra-Patagonian Argentinian record. The Gondwanan Episode is so termed because it is exclusively represented by endemic mammals of Gondwanan origin, i.e., Mesozoic lineages. In contrast, the South American Episode is almost exclusively distinguished by endemic Therian mammals whose ancestors emigrated from the Laurasian North American Continent.

These two major, successive, and for some time superimposed episodes are the result of the geologic history of the South American Plate. (1) This plate was part of the Gondwana Supercontinent until about 120 millions of years before Present (mybP), when it began to separate and drifted westward (but always south and relatively near the North American Plate). Until about 30 mybP it was connected to Western Antarctica, and through it to most of the Eastern Gondwanan continents. (2) By approximately 125 mybP, Donnelly's "Flood Basalt" was initiated. After its cessation by 85 mybP a variety of compressive tectonic features around the Caribbean began, i.e., subduction and island arcs or continental margin magmatism. These features probably permitted the first known inter-American exchange of tetrapods, dinosaurs such as Hadrosauridae from the rising North American continent and Titanosauridae Saltasaurinae from the South American continent. Probably by the latest Cretaceous these geologic features also permitted the immigration of the first Therian, which gave rise to the native South American land mammals. (3) The geologic definition of southern Central America is the last and most important phenomenon related to the final connection of both Americas. By 12 mybP the submarine connection of Central America with South America began, and subsequent volcanic island arcs permitted the beginning of The Great American Biotic Interchange.

According to the Patagonian record, the absence of tribosphenic mammals and the total extinction of the endemic non- and pre-tribosphenic mammals are the most outstanding events characterizing the Gondwanan Episode. Up to the beginning of the South American Episode (early Paleocene), few Gondwanan lineages of mammals (a native Gondwanatheria and an endemic Dryolestoid) survived in the South American continent; another related Gondwanatheria taxon survived up to the Late Eocene in Western Antarctica. These Gondwanan survivors lived together with the first, but advanced, immigrant Therian that initiated the South American Episode. Although not conclusively demonstrated, there are some suggestions that this superposition began earlier, probably by the pre-Campanian Cretaceous. The history of endemic Therian mammals characterizing the South American Episode began to be known in 1948 thanks to the efforts of the Ameghinos and G. G. Simpson. These represented the only known higher taxa until 1985 when Bonaparte recorded the first non-therian Gondwanan lineages in Late Cretaceous (Campanian) Patagonian beds. Successive authors contributed to this history, ratifying Simpson's statement that the South American Cenozoic mammal evolution was episodic. Thus, the most characteristic geobiotic features of the two major episodes are based almost exclusively on the most eloquent Campanian-Quaternary Argentinian record.
Key words: South America, land mammals, evolution, geography, Gondwanan Episode, South American Episode.

Resumen

De acuerdo a registros sin iguales del Cretácico–Cenozoico tardío meridional, la historia de los mamíferos terrestres suramericanos se puede dividir en dos episodios importantes que llamamos el Episodio de Gondwana y el Episodio Suramericano. El primer episodio se distingue por el registro argentino patagónico del norte y centro, mientras que el segundo se basa sobre todo en el registro extra argentino patagónico. El Episodio de Gondwana es así llamado porque está representado

[1] I extend special thanks to Peter Raven for his invitation to be one of the speakers of this symposium. To be selected among such prominent scientists is a great honor, especially by so distinguished an investigator as the Director of the well-known Missouri Botanical Garden. I would like to address a very special acknowledgment to Alan Graham, as well as to Mick Richardson and Victoria Hollowell, whose assistance was not only uncommon but also decisive in making our stay a real pleasure. Without exception, we are also indebted to all the organizers of this pleasant and successful symposium. Special thanks to Olga M. Montiel. Most of the figures were masterfully designed by Agustin Viñas; others by Laura Zampatti, Carlos Vildoso Morales, and Marcela Tomeo. As always, Laura Zampatti contributed to the composition of the paper, suggesting invaluable syntactic ideas. Constructive criticisms and suggestions were made by the referees, Richard Cifelli and Guillermo Rougier, as well by Victoria C. Hollowell (Scientific Editor) and Sophia R. Balcomb (editor); all their suggestions and corrections, without any question, improved this paper. It is obvious that English is not my native language. Hence, I left quite a job for my friend R. Cifelli and the editors!! To all of them, I am very grateful.
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exclusivamente por los mamíferos endémicos de origen gondwánico, i.e., linajes mesozoicos. En contraste, el Episodio Suramericano se distingue casi exclusivamente por mamíferos terios endémicos cuyos antepasados emigraron del continente laurásico norteamericano.

Estos dos episodios importantes, sucesivos y por cierto tiempo sobrepuestos son el resultado de la historia geológica de la placa suramericana. (1) Esta placa formaba parte del supercontinente de Gondwana hasta cerca de 120 maap, cuando comenzó a separarse y desplazarse hacia el oeste (pero siempre al sur y relativamente cerca de la placa norteamericana). Hasta hace cerca de 30 maap estuvo conectada a Antártica occidental, y a través de esta a la mayoría de los continentes gondwánicos orientales. (2) Alrededor de 125 maap, empezó la "inundación basáltica" de Donnelly. Después de su cesación hace 85 maap, comenzó una variedad de características tectónicas compresivas alrededor del Caribe, i.e., arcos de islas y subducción o magmatismo marginal continental. Estas características probablemente permitieron el primer intercambio interamericano conocido de tetrápodos, dinosaurios tales como Hadrosauridae del continente norteamericano en levantamiento y Titanosauridae Saltasaurinae del continente suramericano. Probablemente hacia fines del Cretácico estas características geológicas también permitieron la migración del primer terio, que dio origen a los mamíferos terrestres suramericanos. (3) La definición geológica del sur de América Central es el último y más importante fenómeno relacionado con la conexión final de ambas Américas. Hace 12 maap comenzó la conexión submarina de América Central y del Sur, y subsecuentes arcos de isla volcánicos permitieron el inicio del Gran Intercambio Biótico Americano.

Según el registro patagónico, la ausencia de mamíferos tribosfénicos y la extinción total de los mamíferos endémicos no- y pre-tribosfénicos son los acontecimientos más excepcionales que caracterizan el Episodio de Gondwana. Hasta principio del Episodio Suramericano (Paleoceno temprano), pocos linajes gondwánicos de mamíferos (un Gondwanaterio nativo y un Dryolestoide endémico) sobrevivieron en el continente suramericano; otro taxón Gondwanaterio relacionado sobrevivió hasta el Eoceno tardío en Antártica occidental. Estos sobrevivientes de Gondwana vivieron juntos con el primer, pero avanzado, inmigrante terio que inició el Episodio Suramericano. Aunque no se ha demostrado en forma concluyente, hay algunas sugerencias de que esta superposición comenzó antes, probablemente por el Cretácico pre-Campaniano. La historia de los mamíferos terios endémicos que caracterizan el Episodio Suramericano se empezó a conocer en 1948 gracias a los esfuerzos de los Ameghinos y G. G. Simpson. Estos representaban los únicos taxones avanzados conocidos hasta 1985 cuando Bonaparte registró los primeros linajes no terios de Gondwana en depósitos patagónicos del Cretácico tardío (Campaniano). Autores posteriores contribuyeron a esta historia, ratificando las afirmaciones de Simpson que la evolución de los mamíferos suramericanos cenozoicos fue episódica. Así, las características geobióticas más distintivas de los dos episodios más importantes se basan casi exclusivamente en el más elocuente registro argentino del Campaniano-Cuaternario.

Introduction and Methods

The purpose of this paper is to analyze the first order geologic-geographic phenomena, and the related climatic-environmental changes, that governed the evolutionary history of land mammals recorded to date in the present Patagonian region of the South American continent. This is not a mere analysis of the systematic changes that successively occurred in the mammal communities during the short time that South America was an island continent (a short time because, according to Zachos et al. (2001), the island continent began to be totally isolated from ca. 30 mybP (Fig. 1), not from the beginning of the Cenozoic as Simpson (e.g., 1980) and followers thought). While the history of South American land mammals has been extensively treated, virtually all such treatments were published before recognition of the recently discovered Gondwanan mammals (Campanian and the last earliest Paleocene representatives). Thus, this paper emphasizes the distinct history of the Gondwanan mammal communities with respect to the relatively well-known Cenozoic and Recent South American mammal communities.

The history of South American mammals is something like two histories in one. Within the framework of plate tectonics, varying paleogeographic states divided the history of land mammals recorded in the southern South American continent into two distinct episodes: the Gondwanan Episode and the South American Episode. In fact, the tribosphenic mammals recorded in Late Jurassic beds of the present South American continent (Fig. 2), as well as an advanced pretribosphenic mammal recorded in Early Cretaceous beds (Fig. 3), both in Patagonia, correspond to two somewhat distinct geographical situations when South America was an emerging continent still not well separated from the African continent. Thus, the Gondwanan and South American Episodes are the only two presently well-established major episodes in the history of South American mammals. With that in mind, I will not detail the trends and features of the successive mammal communities as, for example, was done following the previously recognized faunistic cycles (Pascual et al., 1996). For example, within the South American Episode I will only point out the main events that characterize what Stehli and Webb (1985) distinguished as The Great American Biotic Interchange,

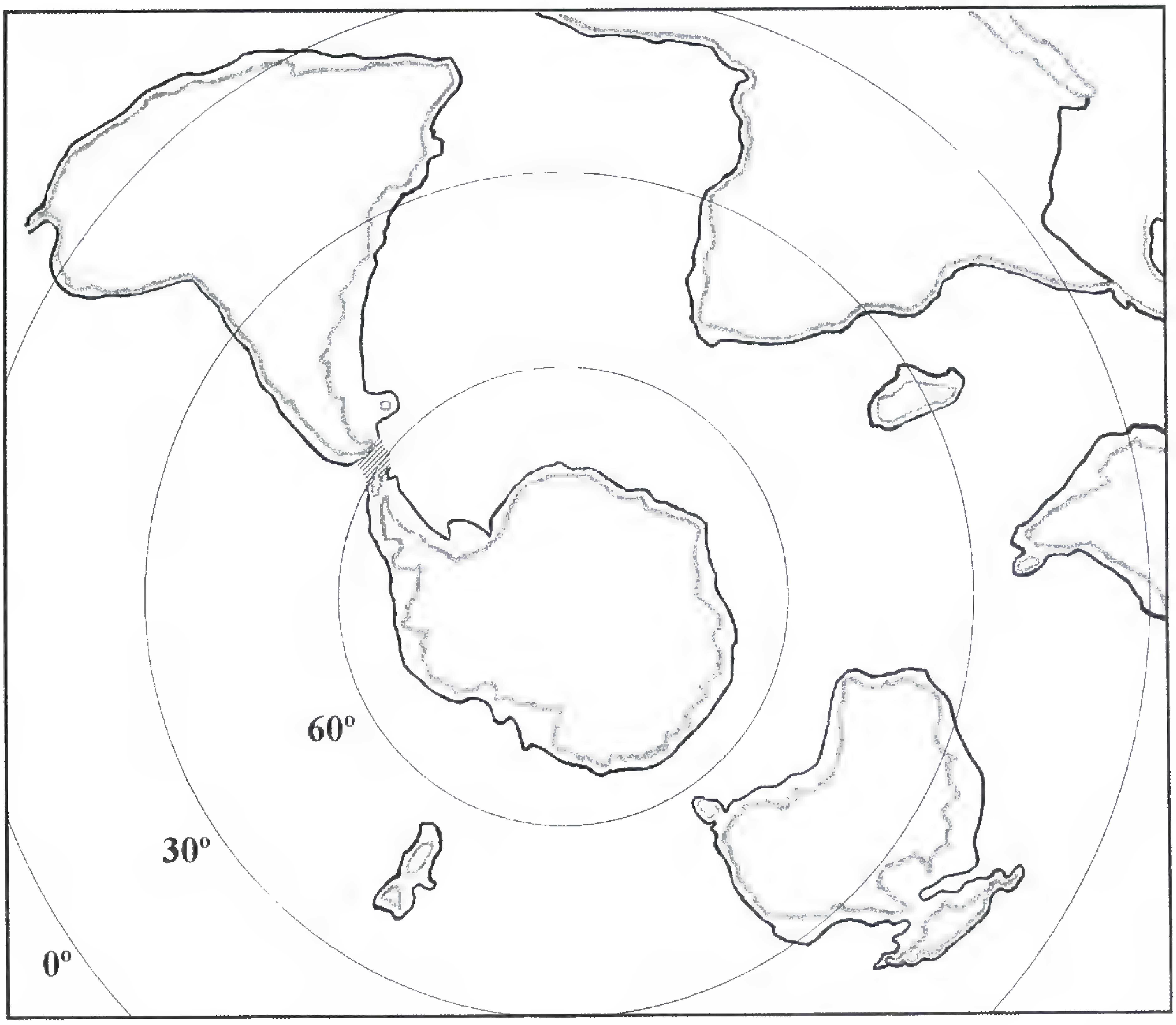


Figure 1. The geographic situation of South America and Antarctica 30 mybP. According to Zachos et al. (2001), these continents were totally separated by this time, thus beginning the transcendental isolation of the South American continent. Land masses 30 mybP are outlined in black.

which has been aptly developed by Webb (2006 this issue) and, independently, but complementarily, by Coates (2003).

As Simpson (1950, 1980) correctly indicated, the history of South American mammals was episodic and divisible into significant intervals of compositional changes, and thus provides the biochronological framework in which to understand their evolution and the evolution of their environments. Because of this, most North and South American paleomammalogists use the Land Mammal Age (LMA)—in our case, the South American Land Mammal Age (SALMA)—as the basic biochronological unit (but see Cione & Tonni, 1995). "Mammal Ages were intended to represent divisions of the Cenozoic, based on characteristic groups of fossil mammals whose temporal relationships and overall stage of evolution were thought to be indicative of a particular interval of geologic time... attention was given to first and last occurrences, 'index fossils' were noted, and characterizing assemblages were listed" (Woodburne, 1987: 1).

The hierarchical arrangement of the SALMAs reveals clusters that represent evolutionary episodes of mammal communities, not only taxonomically, but, more importantly, according to ecological modifications. Ortiz-Jaureguizar (1986) performed a multivariate analysis of similarity among SALMAs, a method that was subsequently revisited and updated by Pascual & Ortiz-Jaureguizar (1990) and Pascual et al. (1996). As Ortiz-Jaureguizar (1986) did, these latter authors used SALMAs as operational taxonomic units (OTUs) and families of the Late Cretaceous and Cenozoic Land-Mammal Ages as "characters." They were able to recognize four hierarchical ranks of SALMA organization, distinguished as Faunistic Units; from lower to higher these were Faunistic Subcycles, Faunistic Cycles, Faunistic Supercyles, and Faunistic Megacycles (Table 1). Major changes observed among mammal communities (Pascual & Ortiz-Jaureguizar, 1990; Pascual et al., 1996; Pascual, 2001) appear to be concomitantly related to major environmental changes, apparently correlated with

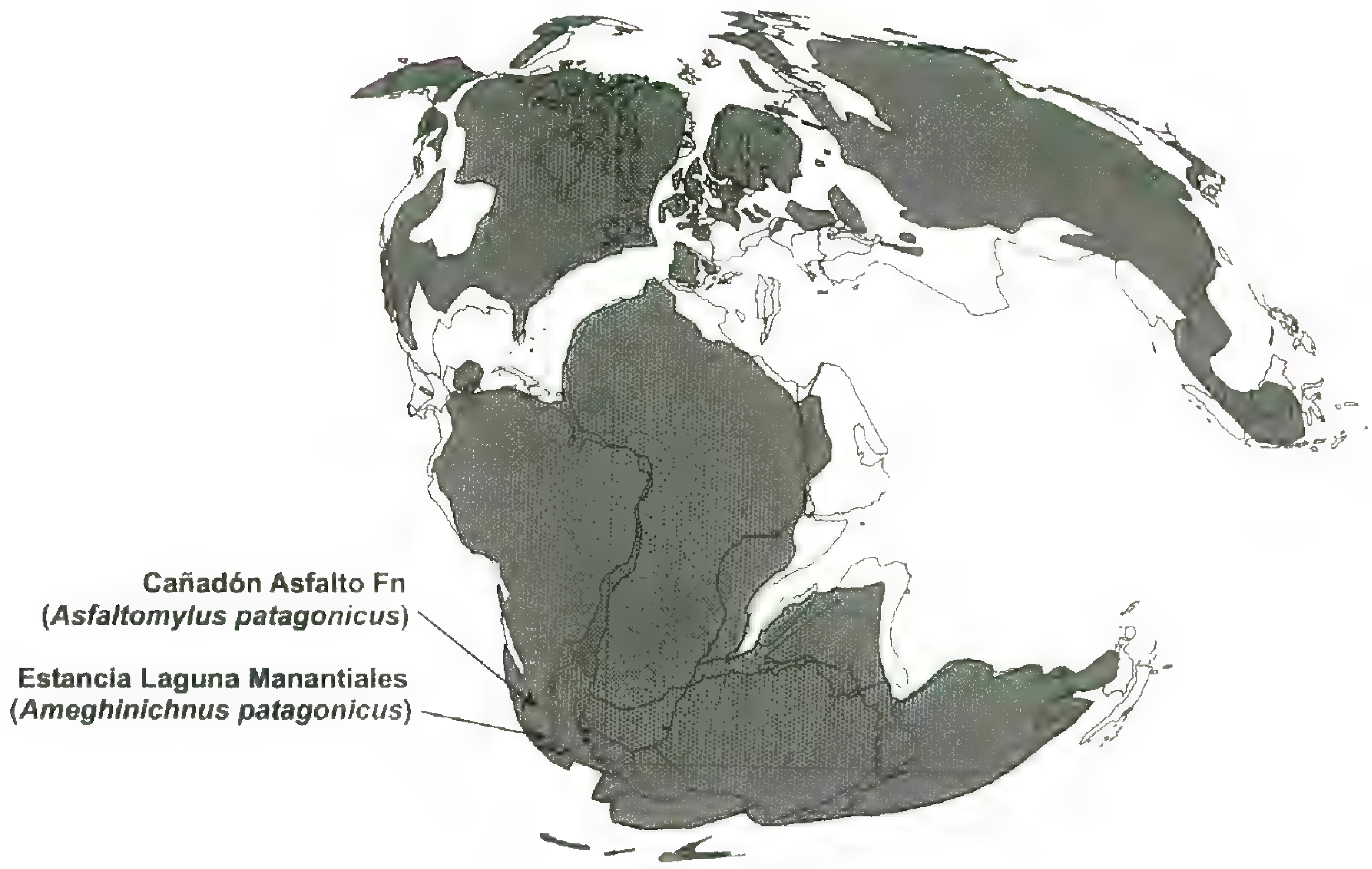


Figure 2. The paleogeographic situation of the South American continent by the end of the Jurassic, 155 mybP, i.e., still connected to the remaining Gondwanan continents (*fide* Smith et al., 1994). This apparently explains the persistence of Eutherian mammals in what was going to be the Patagonian territory, and their absence during the Patagonian Late Cretaceous Gondwanan Episode. *Asfaltomylus patagonicus* Rauhut, Martin, Ortiz-Jaureguizar & Puerta, 2002 is a Late Jurassic tribosphenic mammal found in Patagonia (Chubut), and *Ameghinichnus patagonicus* Casamiquela, 1961 is a Late Jurassic ichnita of a supposed Pantotheria, also from Patagonia (Santa Cruz). Grey shading represents land masses 155 mybP. (Modified from Smith et al., 1994; reprinted with the permission of Cambridge University Press.)

worldwide diastrophic phenomena. We use diastrophic phenomena in its most comprehensive sense including the fragmentation and drifting of continents, sea level changes, etc. We recently (Pascual & Ortiz-Jaureguizar, 1992; Pascual et al., 1996; Pascual & Ortiz-Jaureguizar, in press) also applied this biochronological classification to Late Cretaceous mammal communities from Patagonia known to date (Scillato-Yané & Pascual, 1984, 1985; Bonaparte et al., 1993), including the recently discovered, earliest mammal-bearing Paleocene formation that documents the last known Gondwanan survivors. To avoid repetition, and

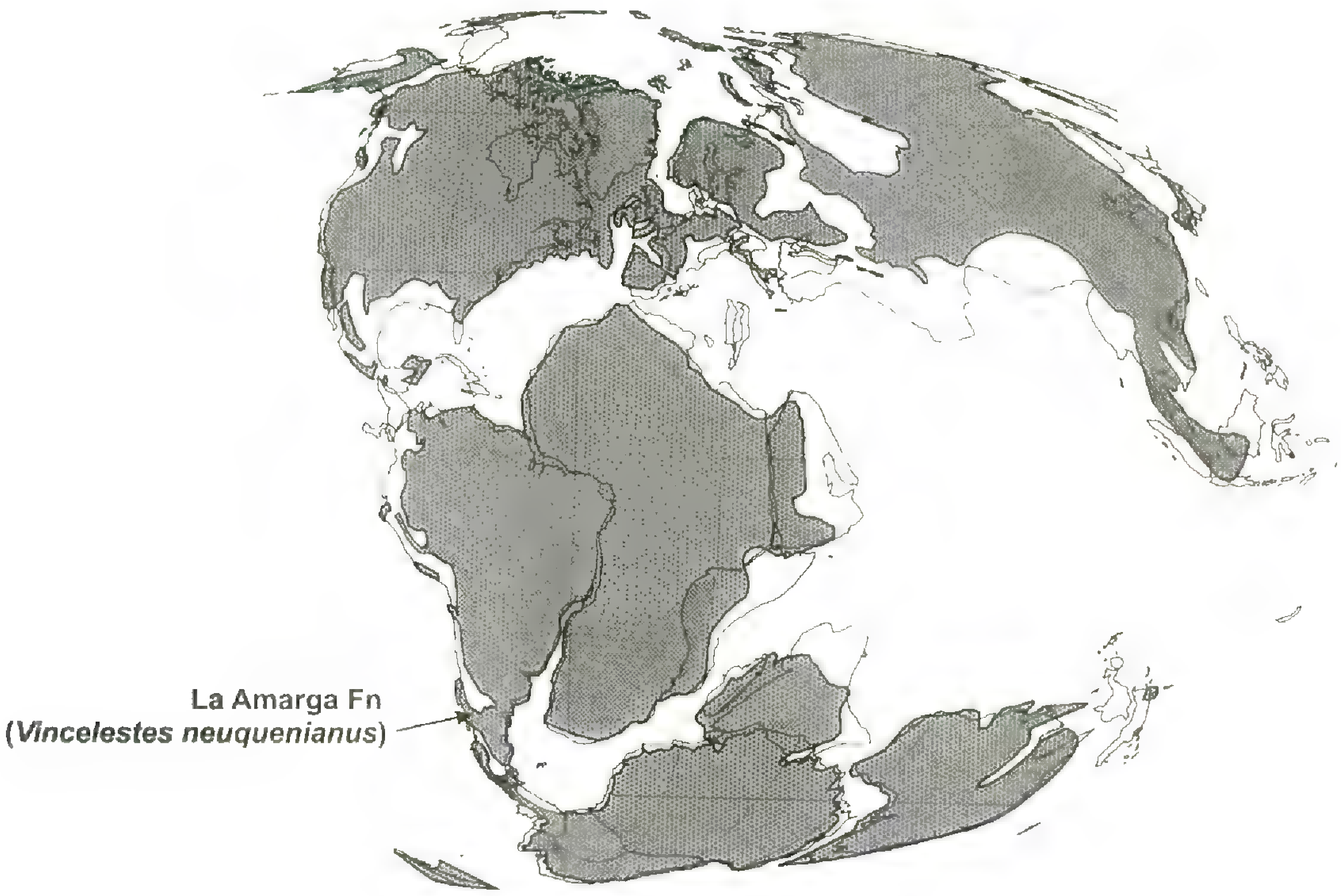
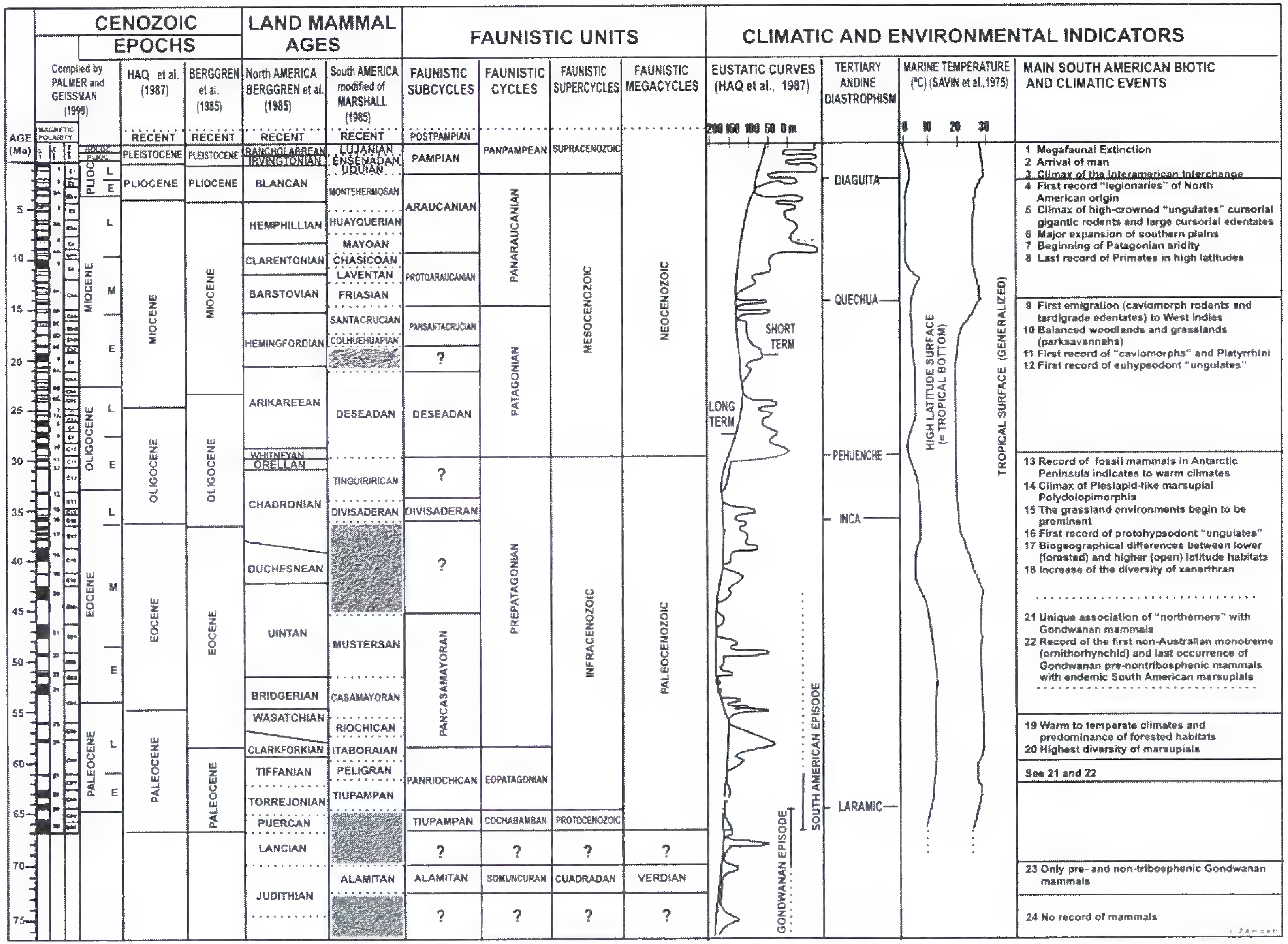


Figure 3. The primordial South American and African continents had somewhat drifted apart but were still tenuously connected by 135 mybP. This explains why the Early Cretaceous *Vincelestes neuquenianus*, recorded in the northwestern Patagonian bed of La Amarga Formation, is not part of the Gondwanan Episode. Grey shading represents land masses 135 mybP. (Modified from Smith et al., 1994; reprinted with the permission of Cambridge University Press.)

Table 1. Land-mammal Ages: dates, faunistic units, and the main climatic and environmental indicators.



to provide a synopsis of essential features, I herein summarize the main evolutionary events that mark the history of South American mammals according to the higher Faunistic Cycles (Table 1), although in some cases transcendental events punctuate these inclusive Faunistic Cycles and Subcycles.

Antecedents

None of the three of the most outstanding connaisseurs of the South American extinct and extant land mammals, Carlos and Florentino Ameghinos (see Simpson, 1948: 19–26) and G. G. Simpson (1980), were aware of the recently incorporated South American Mesozoic mammals. However, F. Ameghino and Simpson, based on distinct, supposedly positive, evidence, did consider that they knew them. For example, C. Ameghinos found dinosaur-like teeth associated with mammals of Casamayoran age (early Eocene) in central Patagonia (Ameghino, 1906). F. Ameghino interpreted these zyphodont teeth as pertaining to a carnivorous dinosaur (Ameghino, 1906). Simpson (1932, 1933, and particularly, 1937a, 1937b), using relatively complete, and different, remains, demonstrated that these teeth pertained to a curious and unique terrestrial crocodilian species, which he named *Sebecus icaeorhinus* Simpson and included in a new peculiar infraorder he named Sebecosuchia (Simpson, 1937a). In 1946, E. H. Colbert accepted Simpson's request to finish his study and published a monographic study on the best specimens collected by Simpson and his staff of the American Museum of Natural History of New York (Colbert, 1946). Colbert corroborated both the crocodilian nature of this specimen and that it was stratigraphically associated with mammals of Eocene age (Casamayoran SALMA). However, even at the time he studied those crocodilian remains, he considered the relationships of this new crocodile to be questionable (Colbert, 1946; see also the conclusions of Gasparini, 1984).

Of course Simpson's papers, and Colbert's conclusive paper, were unknown to F. Ameghino, who died in 1911 thinking that supposedly carnivorous dinosaurs lived in South America during the Cretaceous and were associated with more advanced mammals than were known from anywhere else in the world. Consequently, he regarded these mammal-bearing beds with supposedly carnivorous dinosaur teeth as Cretaceous in age, whereas Simpson later considered these beds to be Eocene in age (Simpson, 1937a), representing the Casamayoran SALMA (Table 1).

The transcending point is that, on this basis, F. Ameghino built a chronological scale that was too old and which he used as standard not only for South American land mammal-bearing beds but also for all related lithostratigraphical units (Ameghino, 1906). This was his *péché originale*, which so negatively influenced his otherwise extraordinary work. This transcendent error produced an almost universal reaction against him, especially when he suggestively named monkey (Ceboidea) remains, found in what he took as early Eocene beds of Patagonia, *Homunculus patagonicus* Ameghino (Ameghino, 1891). About this species he wrote "...es un mono de caracteres muy elevados, y lo considero como formando parte de la línea que conduce al hombre y a los antropomorfos" (Ameghino, 1891: 291).

Simpson (1980), in turn, accepted the Cretaceous age of the mammal-bearing Umayo Formation discovered by the French paleontologist B. Sigé (Grambast et al., 1967; Sigé, 1972) in the southern Peruvian Andes. These French paleontologists correlated this formation with the marine Vilquechico Formation, exposed further to the north and undoubtedly Cretaceous in age, and wrongly used the same name. The mammals collected in the Umayo Formation were later demonstrated to be early Paleocene, not Cretaceous, in age (Crochet, 1979). What Simpson (1980: 39) expressed about these Peruvian mammals is quite instructive: "... it would have been expected that mammals like these would occur in the Cretaceous of South America." Simpson did not admit that non-tribosphenic and pre-tribosphenic mammals were inhabitants, at least, during the Late Cretaceous of the South American continent, and by extension—considering his non-acceptance of the Plate Tectonic rationale—that what we presently accept as the Gondwana supercontinent had no such pre-Cenozoic mammals as inhabitants.

It has to be remarked that what was known by Simpson (Simpson, 1980) as the "curious history" of South American mammals was based only on the endemic Cenozoic mammals, the majority of which descended from Laurasian mammal immigrants from the primordial North American continent. No Gondwanan mammal was known until the 1980s, when Bonaparte and staff (Bonaparte et al., 1984; Bonaparte & Soria, 1985; Bonaparte, 1986a, 1986b, 1988, 1990, 1996) found the first unquestionable Late Cretaceous mammals, and simultaneously Pascual and staff (e.g., Scillato-Yané & Pascual, 1984, 1985) found the last relictual representatives, also in Patagonia but in beds of early Paleocene age. None of the relatively well known Cenozoic and living mammals show features indicating a Gondwanan ancestry.

The Gondwanan mammals completely disappeared by the early Paleocene, at least in Southern South America, in contrast to what happened, for example, with the Monotremata in Australia. Probable Gond-

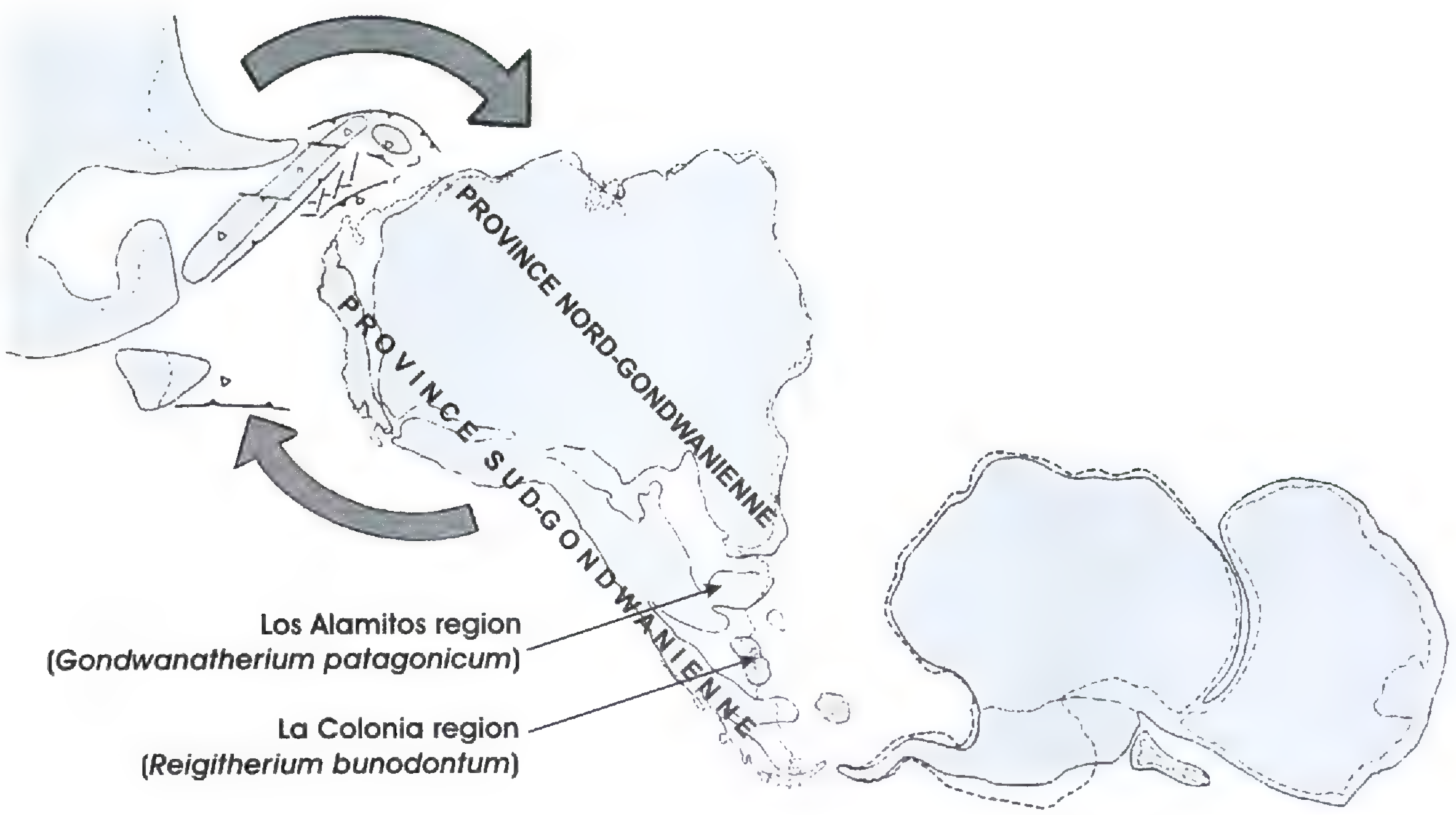


Figure 4. Between 85 and 63 mybP a seaway bisected the South American continent into two paleobiogeographic provinces (*fide* Broin & de la Fuente, 1993). It is likely that most of this interval was the climax of the Gondwanan Episode, and by its end the first Therian immigrants from North America inaugurated the South American Episode. Los Alamitos region and La Colonia region are the two coetaneous Campanian Patagonian localities where the two indicated Gondwanan taxa were found.

wanan survival candidates are the Xenarthra, despite the fact that none have yet been found in South American Late Cretaceous or earliest Paleocene beds.

Consequently, Simpson's (Simpson, 1950: 363) interpretation of what he termed "episodic history" of South American mammals was correct, but only applicable to the Cenozoic mammals of which he was knowledgeable.

Discussion

The best current Mesozoic record of South American land mammals is almost exclusively Patagonian and Late Cretaceous (Campanian) in age (Fig. 4). Compared to the Cenozoic record from the entire continent, the Late Cretacaeous evidence demonstrates that the entire South American land mammal history is radically divided into two major and unrelated episodes occurring under two distinct geographic sceneries. These two distinctive episodes were separated by a relatively long Maastrichtian–early Paleocene hiatus; there is only one dubious early Paleocene Patagonian specimen, a tribosphenic molar found quite recently (Goin et al., 2005). This molar may well represent one of the oldest therians to have emigrated from Laurasia, embodying the beginning of The South American Episode. Additionally, an assemblage from Bolivia, of middle Maastrichtian age based on interbedded marine taxa, includes an undoubtedly eutherian mammal, based on a molarized premolar (*non vidi, fide* Gayet et al., 2001). This may well represent the Ancient Immigrants from North America that inaugurated the South American Episode. We originally recognized those two major episodes as stages, plus a third, the Late Pleistocene "Neotropical Stage" (Pascual, 1996, 1998; Vizcaíno et al., 1998: 202). However, herein I recognize those two major and well distinguishable episodes as The Gondwanan Episode and The South American Episode.

The Gondwanan Episode

To date, the Gondwanan Episode is best represented by mammalian remains from two middle Patagonian localities, both Late Cretaceous in age (Los Alamitos and La Colonia, Chubut; Fig. 4). Both Patagonian Late Cretaceous mammal assemblages (apparently Campanian) are comprised only of non-tribosphenic and pre-tribosphenic mammals.

Based on the Patagonian records, and the Bolivian one (Patcha Pata) mentioned above (if the supposed eutherian is really of Gondwanan origin), The Gondwanan Episode extended from the latest Cretaceous (Campanian) to earliest Paleocene (Danian) interval, and thus far is represented only in these two central Patagonian localities, and probably Bolivia. Similar stratigraphic sequences and land mammal

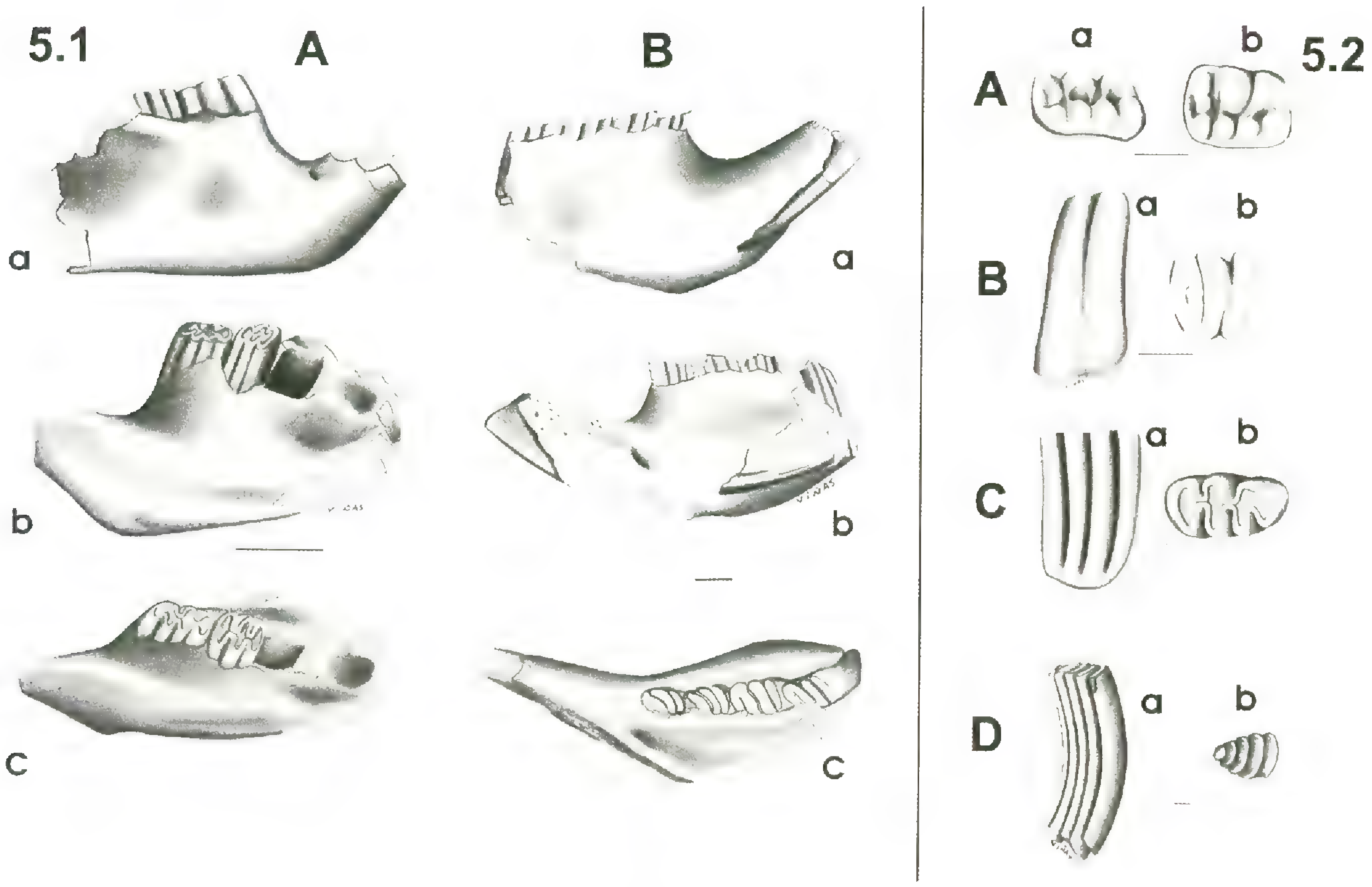


Figure 5.1. A comparison of right dentaries in (a) labial, (b) lingual, and (c) occlusal views of (A) the early Paleocene Gondwanatheria *Sudamerica ameghinoi* Scillato Yané & Pascual, 1984 with (B) the Late Miocene caviomorph rodent Dinomyidae *Tetrastylus* Ameghino, 1886 sp. Scale bars: 1 cm. Figure 5.2. A comparison of the homologous left m1 of the Gondwanatherians (A) *Ferugliotherium windhauseni* Bonaparte, (B) *Gondwanatherium patagonicum* Bonaparte, and (C) *Sudamerica ameghinoi* with the late Miocene caviomorph rodent Dinomyidae (D) *Pentastilomys* Kraglievich, 1926. Scale bars: 1 mm.

genera present at both Patagonian localities indicate synchronicity, representing continental facies of a wide-ranging epeirogenic marine Campanian-Danian transgression (Bonaparte, 1987a, 1987b, 1996; Pascual et al., 2000a; Fig. 4). This transgression extended along the length of the eastern region of the Andes, as far as the Bolivian Lake Titicaca. During the Campanian a coetaneous "Caribbean" transgression connected to the former by the Titicaca region, which, as a seaway, divided the South American territory into two Late Cretaceous–early Paleocene terrestrial biogeographical provinces ("province nord-gondwanienne" and "province sud-gondwanienne," sensu Broin & de la Fuente, 1993), verified by various abiotic and biotic evidences (Wilson & Arens, 2001: Fig. 4).

The Patagonian Late Cretaceous record (the most informative and eloquently representative base of the Gondwanan Episode) shows the total absence of tribosphenic mammals. This absence and the advanced morphology and endemism of non-tribosphenic and pre-tribosphenic mammals illustrate the most important mammalian evolutionary processes that occurred in Patagonia during the Gondwanan Episode. For example, among the non-tribosphenic taxa were the quite derived Gondwanatheria, together with dubious Laurasian Triconodonta, Symmetrodonta, and Docodonta, plus an array of quite advanced Dryolestoidea (Figs. 5, 6). The record of the Bolivian Maastrichtian Eutherian (see above) may indicate that this is not a valid generalization for the whole continent, and that Patagonia—as insinuated by some other fossil vertebrates (see below)—may have had a distinct biogeographic history, at least from the second half of the Mesozoic to the Present. In any case, this does not refute the existence of the two distinct major episodes that characterized the South American land mammal history.

Bonaparte (1988) discovered an Early Cretaceous mammal, *Vincelestes neuquenianus* Bonaparte, from another north western Patagonian locality (Fig. 3), which he considered to be Eupantotherian. To Bonaparte and Rougier (1987), Butler (1990), and Rougier et al. (1992), the level of organization of its molars appeared to be "...between the Late Jurassic *Peramus* Owen and the Early Cretaceous *Aegialodon* Kermack, Lees & Mussett" (Butler, 1990: 542). Therefore, the character states of *V. neuquenianus* placed it in an intermediate state between "non-therian" mammals and Therian taxa. Thus, Rougier (1993) grouped this advanced taxon with therians in a clade he named Prototribosphenida. Two additional

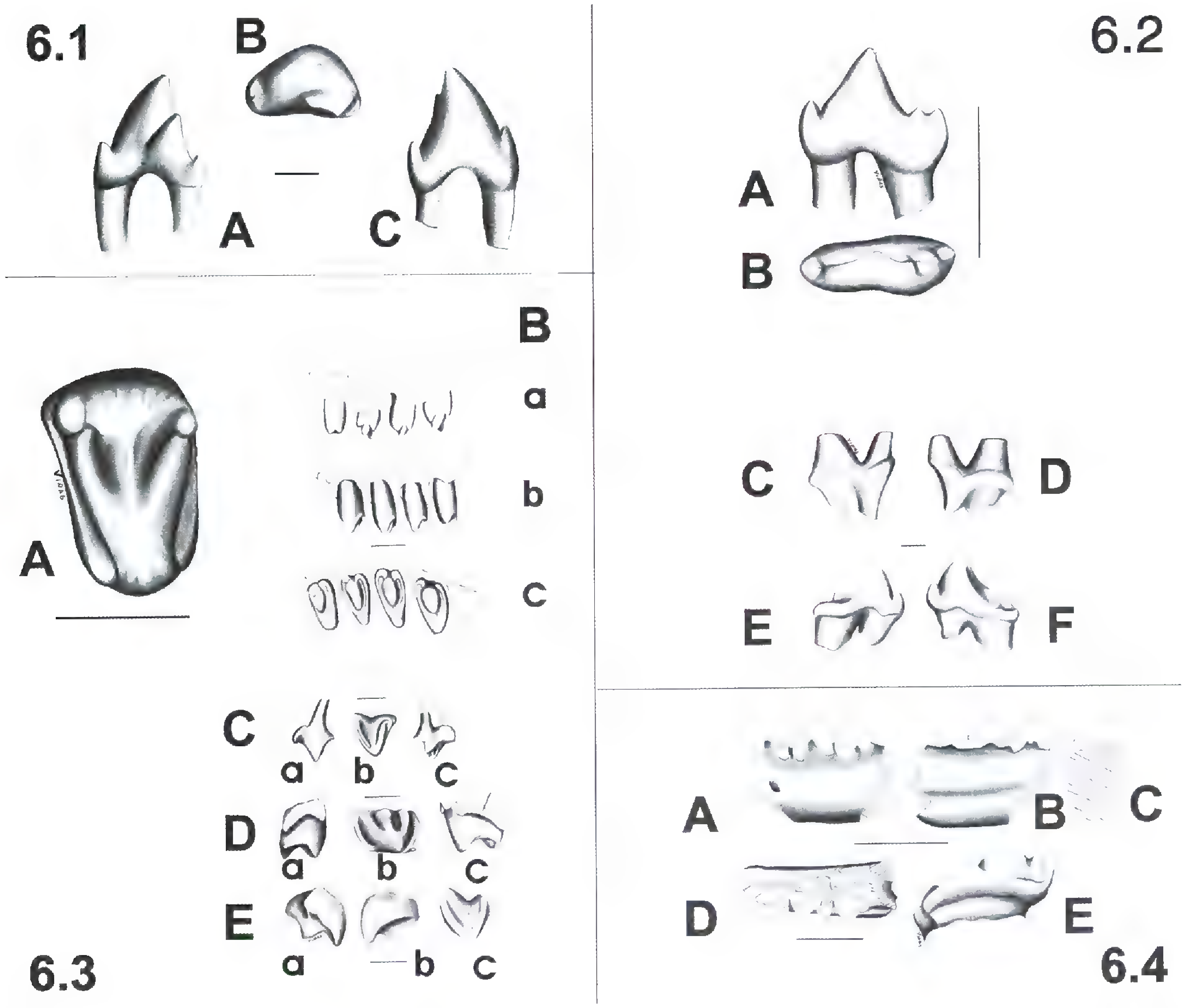


Figure 6. Upper and lower molars of the most conspicuous non-therians characteristic of the Gondwanan Episode. **6.1** Symmetrodonta. *Bondesius ferox* Bonaparte: (A) lingual, (B) occlusal, and (C) labial views of a right lower molar. **6.2.** Triconodonta. *Austrotriconodon mckennai* Bonaparte: (A) labial and (B) occlusal views of a lower molar. *Austrotriconodon sepulvedai* Bonaparte (Triconodonta?): (C) labial and (D) lingual views of a right upper molar, and (E) labial and (F) lingual views of a right lower molar. **6.3.** Dryolestoidea. Upper molars of (A) *Mesungulatum houssayi* Bonaparte & Soria, occlusal view; (B) *Leonardus cuspidatus* Bonaparte: (a) labial, (b) lingual, and (c) occlusal views; (C) *Brandonia intermedia* Bonaparte: (a) labial, (b) occlusal, and (c) lingual views; (D) *Paraungulatum rectangularis* Bonaparte: (a) distal, (b) occlusal, and (c) mesial views; (E) *Casamiquelia rionegrina* Bonaparte: (a) mesial, (b) distal, and (c) occlusal views. **6.4** Docodonta? *Reigitherium bunodontum* Bonaparte. Fragment of a left dentary: (A) labial, (B) lingual, and (D) occlusal views of premolar 1–molar 2, (C) posterior view behind molar 2, and (E) distal view of molar 2.

mammals, from two more distant Late Jurassic localities, also in Patagonia (Casamiquela, 1961; Rauhut et al., 2002; Fig. 2), as well as two Late Triassic–Early Jurassic mammal-bearing Brazilian localities (Ribeiro et al., 2001; Bonaparte et al., 2003), suggest that there were at least two more Mesozoic minor "episodes," though they are not well known to date. Supporting those Early Cretaceous and Late Jurassic minor "episodes," the paleogeographic evidence shows that these mammals evolved in different geographic situations. During the Late Triassic, what was going to be the South American continent was connected, on the one hand, to what was going to be the North American continent, and, on the other hand, to what was going to be the Gondwanan Supercontinent (*fide* Smith et al., 1994, fig. 29). By the Late Jurassic what was going to be the South American continent was already separated from what was going to be the North American continent, but still connected to Africa (Fig. 2) as part of the Gondwanan Supercontinent. By the Early Cretaceous, southern South America and Africa were already separating, with the northern sector somewhat drifted but still tenuously connected (Fig. 3; see also Storey, 1995, fig. 2c; compare these two figures with Fig. 1). The extinction of most of the Gondwanan mammals, as well as the extinction of the relictual earliest Paleocene taxa, must have occurred while the South American continent lay in the geographical position depicted in Figure 4, i.e., south of and near to the

North American continent, but still connected to the Australian continent.

The seaway mentioned above existed between ca. 80 and 64 mybP and bisected the pre-South American continent into the two biogeographic provinces, as recognized by Broin and de la Fuente (1993: 211–214) on the basis of distinct chelonian faunae: "province nord-gondwanienne" dominated by the Pelomesudae and "province sud-gondwanienne" dominated by the Chelidae. Notably, the former were, and are, well represented in the Atlantic border of equatorial Africa while the latter were, and are, common inhabitants of the Australian continent. The dipnoan fishes offer another, similar testimony: Lepidosirenidae (*Lepidosiren* Fitzinger in the province nord-gondwanienne vs. *Protopterus* Owen in intertropical Africa) and Ceratodontidae in the province sud-gondwanienne (plus *Ceratodus* Agassiz in the Late Cretaceous of Patagonia vs. *Neoceratodus* de Castelnau presently in Australia) (see Fernández et al., 1973; Pascual & Bondesio, 1976; Bondesio & Pascual, 1977).

The Late Cretaceous mammal-bearing sediments from Patagonia, representing the Gondwanan Episode, are continental facies of that southern marine seaway. The faunal biota of the province nord-gondwanienne closely resembles other Gondwanan equatorial faunal biotas, such as that from northern Africa, which, in turn, are distinct from the southern South American faunal biota that more closely resemble other austral Gondwanan faunal biotas, such as those from Antarctica and Australia (Zinsmeister, 1987; Pascual et al., 1992b, 1996). For example, the Lepidosirenidae lung-fishes during the Cretaceous were, and still are, endemic to the province nord-gondwanienne and northern Africa. This is also the case for the Chelidae turtles which are endemic to the province sud-gondwanienne and southern Africa. Similarly, the Ceratodontidae lung-fishes and the Chelidae turtles were endemic to Patagonia during the Cretaceous and are presently endemic to Australia. Crisci et al. (1991) discuss many other examples of living Insecta, Fungii, Gymnosperma, and Angiosperma, which have similar vicariant distributions in southern South America and the continents that were part of Eastern Gondwana. The hypothesis about the existence of a South American Late Cretaceous–Paleocene province nord-gondwanienne and province sud-gondwanienne was tested and confirmed by a quantitative comparison of Late Cretaceous and Paleocene palynofloras, distinct biotic elements, from austral and equatorial South American representatives (Wilson & Arens, 2001).

By the time of The Gondwanan Episode, the future South American continent was still somewhat connected to Antarctica and had drifted to just south of, and nearer to, the rising North American continent, with some archipelagic volcanic islands between each continent (Fig. 4). As a Noah's Ark (sensu McKenna, 1972), the South American Plate had been carrying relictual Gondwanan mammals. This is supported by remains from the Patagonian Los Alamitos Formation (Campanian–Maastrichtian; Bonaparte 1996), as well as those in the correlated La Colonia Formation (Pascual et al., 2000b, 2002; Figs. 5, 6). It is impossible to know when the massive extinction of Gondwanan mammals began. The separated South American continent, always situated south of the North American Plate, drifted north-northwest until the Campanian, when its mutual connection by the Panamanian "Bridge" began (cf. Figs. 2–4). As pointed out above, the complete extinction definitely occurred while the continent was already situated near to and south of the North American continent, not very far from its present position, around 80 mybP. At this time, the Caribbean sea was not yet defined, although intermediate volcanic islands enabled the first interamerican faunal exchange (Fig. 12): hadrosaurid dinosaurs from the rising North American continent and titanosaurid saltasaurine dinosaurs from the South American continent.

Closely related Gondwanatherians found in Late Cretaceous beds of Madagascar and peninsular India (Krause et al., 1997) also appear to be relictual Gondwanan mammals; they likewise survived on Noah's Ark–like continents (Fig. 7) that resulted from fragmentation of the Gondwanan Supercontinent.

THE SOUTH AMERICAN EPISODE

The last steps of The First Great Turnover (sensu Pascual et al., 2001) must have occurred during a hiatus which spanned the Maastrichtian–earliest Paleocene. This involved the extinction of all the Gondwanan mammals and their "replacement" by Laurasian therians, which emigrated from the North American sector. Apparently this marked extinction was another effect of the massive Cretaceous–Cenozoic extinction. This event marks the end of The Gondwanan Episode just as the subsequent Laurasian therian immigration marks the beginning of the South American Episode. Both episodes occurred some time during the latest Cretaceous–earliest Paleocene span, as evidenced by records in the middle Patagonian Hansen Member—usually known as Banco Negro Inferior—of the marine Salamanca Formation (early Paleocene), exposed in the coastal region of San Jorge Gulf, ca. 20 km north of Comodoro Rivadavia (Chubut) (Scillato-Yané & Pascual, 1984, 1985; Pascual et al., 1992a, 1992b, 1999; Bonaparte et al., 1993; Gelfo & Pascual, 2001; See map in Pascual et al., 1992b).

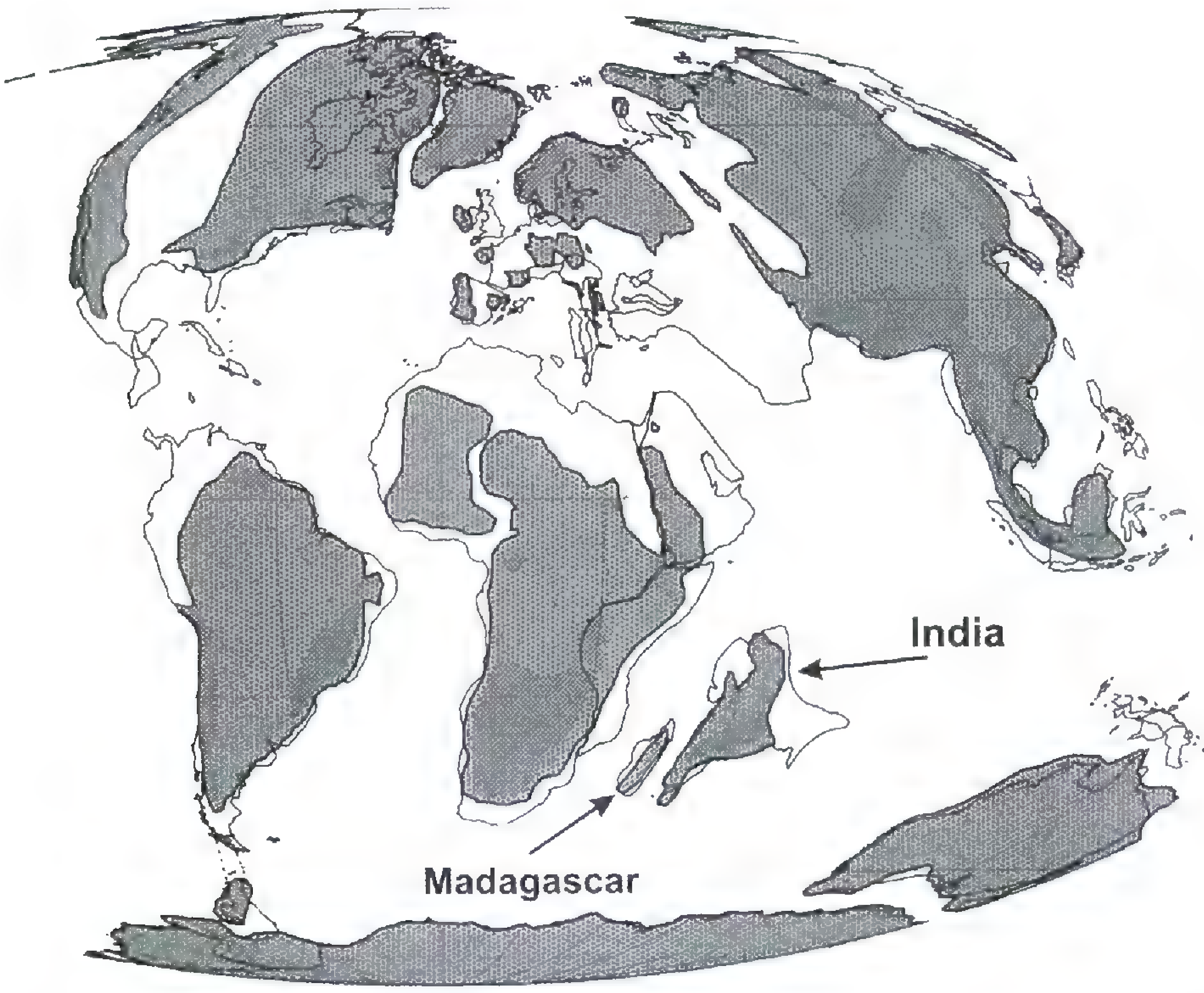


Figure 7. By aproximately 80 mybP Madagascar and India, as Noah's Ark–like continents, kept living Late Cretaceous Gondwanatherians, similar to the South American early Paleocene *Sudamerica ameghinoi*. Grey shading represents land masses 80 mybP. (Modified from Smith et al., 1994; reprinted with the permission of Cambridge University Press.)

An older Paleocene isolated, tribosphenic molar recently found by Goin et al. (Goin et al., 2005) in the Danian Lefipán Formation from central-western Patagonia appears to be the oldest known Laurasian immigrant to South America, even older than the Laurasian immigrants found in northern Bolivian beds of the Tiupampan SALMA (early Paleocene, although not earliest; see Muizon, 1991). Examples of Laurasian immigrants that inaugurated the subsequent South American Episode include the Marsupialia, Borhyaenoidea, Borhyaenidae (*Mayulestes* de Muizon), Peradectidae (*Peradectes* Matthew & Granger), Caroloameghiniidae (*Robertohoffstetteria* Marshall, de Muizon & Sige), Didelphidae (*Andinodelphis* Marshall & de Muizon, *Incadelphys* Marshall & de Muizon, *Mizquedelphy* Marshall & de Muizon, *Pucadelphis* Marshall & de Muizon, *Carolopaulacoutia* (Mckenna & Bell)(=*Sternbergia* Paula Couto), *Jaskhadelphys* Marshall & de Muizon, *Chulpasia* Crochet & Sigè, *Khasia* Marshall & de Muizon, *Sillustania* Crochet and Sige) as well as the Placentalia Leptictida (Palaeoryctidae?, cf. *Cimolestes* Marsh), Condylarthra, Hyopsodontidae (*Andinodus* de Muizon & Marshall), Mioclaenidae (*Kollpania* Marshall & de Muizon, *Molinodus* de Muizon & Marshall, *Pucanodus* de Muizon & Marshall, *Simoclaenus* de Muizon & Cifelli, *Tiuclaenus* de Muizon & Marshall), Periptichidae (*Mimamuta* Van Valen), and Pantodonta (*Alcidedorbignya inopinata* de Muizon & Marshall) (but see Bertini et al., 1993, and Gayet et al., 2001).

The tribosphenic molar from the Lefipan Formation appears to be older than the Australian and Laurasian immigrants recorded in the Patagonian Peligran Land Mammal Age beds (see Pascual et al., 1992a, 1992b; Bonaparte et al., 1993; Forasiepi & Martinelli, 2003; Pascual & Ortiz-Jaureguizar, submitted to press). These immigrants include the Platypoda, Ornithorhynchidae (*Monotrematum* Pascual, Archer, Ortiz Jaureguizar, Prado, Godthelp & Hand; Fig. 8); the Marsupialia, Didelphimorphia, Didephidae (*Derorhynchus* Paula Couto, *Didelphopsis* Paula Couto), the Polydolopimorpha, Bonapartheriidae (*Bonapartherium* Pascual), Polydolopidae gen. nov.; as well as the Placentalia, Condylarthra, Mioclaenidae (*Escribania* Bonaparte, Van Valen & Kramartz, *Raulvaccia* Bonaparte, Van Valen & Kramartz), Notopterna Notonychopidae (*Resquisia* Bonaparte and Morales).

In summary, the mammal from the Paleocene Patagonian Lefipan Formation plus the taxa from the Bolivian Tiupampan and the Patagonian Peligran appear to be among the oldest Laurasian immigrants, i.e., Simpson's (1950) Ancient Immigrants. These taxa evolved on a proto-South American substratum that included at least the Antarctic Peninsula (Fig. 8) up to about 30 mybP (Fig. 9). At the beginning of the South American Episode (early Paleocene) two Gondwanan relictual taxa, a gondwanatherian and a dryolestoid, as well as the first and unique immigrant of an Australian ornithorhynchid monotreme, persisted in central Patagonia (Fig. 8). Another relictual Gondwanan mammal was an Eocene gonwanatherian, found in the Antarctic Peninsula (Reguero et al., 2002). The Patagonian mammals of the Peligran SALMA (early Paleocene) suggest that the basic

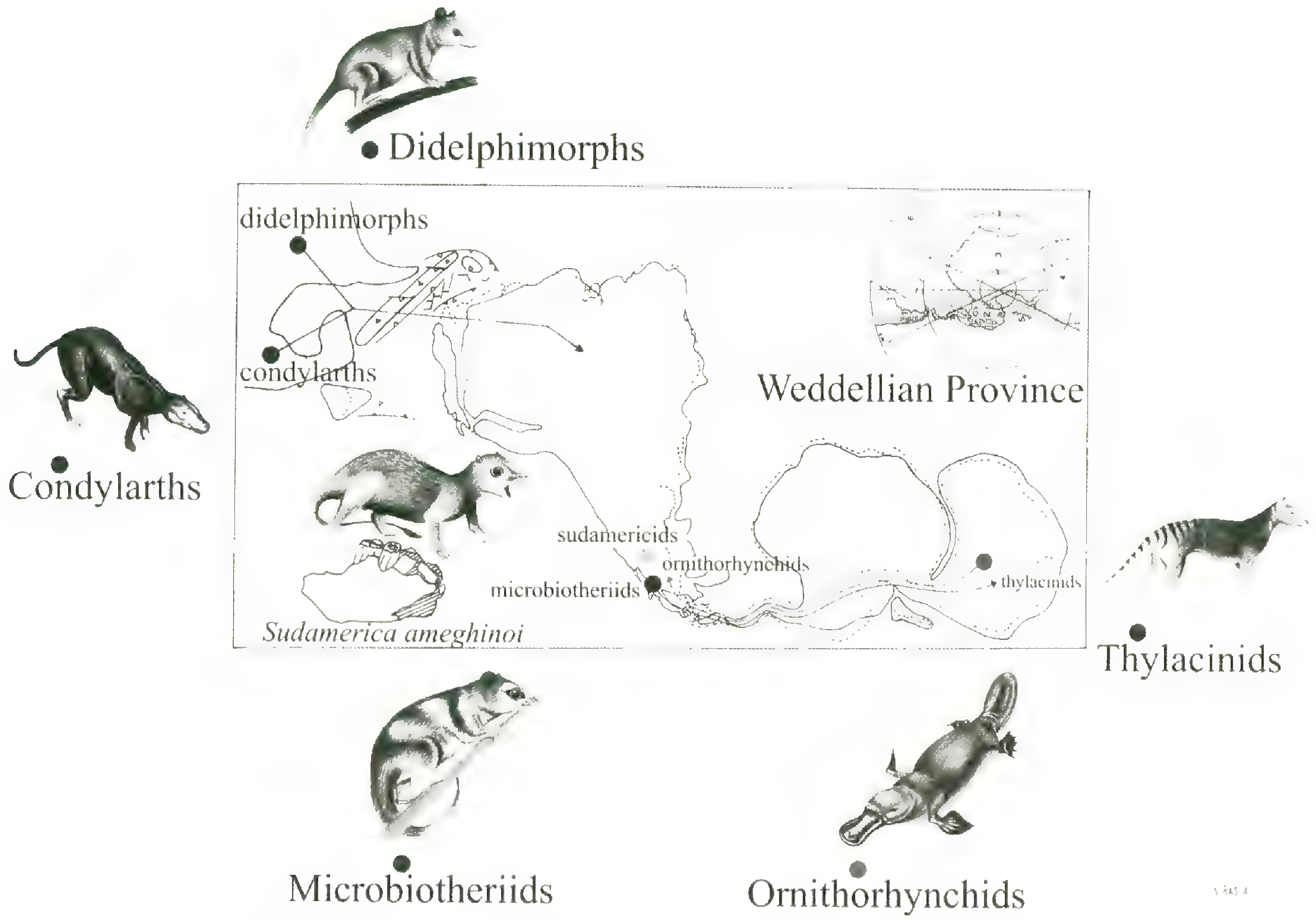


Figure 8. Inferred geographic relationships of the primordial South American continent between 85 and 63 mybP. The South American Episode began during the Late Cretaceous when the South American continent was still connected to Antarctica, i.e., not yet completely isolated. The first known immigrant tetrapod from North America was the Campanian dinosaur Hadrosauridae *Krytosaurus* Brown, 1910 sp. Probably by the Late Cretaceous, and certainly by the early Paleocene, it was followed by Metatherian and Eutherian mammals, ancestors of the taxa depicted here. However, their immigration may have begun by the pre-Campanian Late Cretaceous. By the Late Cretaceous, marsupials emigrated to Australia and, following the same route, by the early Paleocene, South America received the first Australian immigrant, the monotreme ornithorhynchid *Monotrematum sudamericanum* Pascual, Archer, Ortiz Jaureguizar, Prado, Godthelp & Hand, 1992b. Dark grey bullets and arrow indicate the first immigrants from North America to South America. Among them the microbiotheriids were the first marsupials to emigrate from South America to Australia, through the Antarctic continent. Thylacinids are one of the end products differentiated in Australia from South American marsupials (Sparassodonta?). *Sudamerica ameghinoi* Scillato Yané & Pascual, 1984 is the first and last Gondwanatheria found in Late Cretaceous and early Paleocene beds from Patagonia. Ornithorhynchids are the first monotreme found outside (Late Cretaceous–early Paleocene of Patagonia) of Australasia.

diversification of the immigrant therians was well on its way. If those therian mammals recorded by Bertini et al. (1993) and Gayet et al. (2001) really were of Late Cretaceous age and immigrants from Laurasia (North America), then they are the oldest known immigrants, i.e., Simpson's (1950) Ancient Immigrants.

In accordance with the main turnovers withstood by the Cenozoic land-mammal communities, otherwise related to first order diastrophic and climatic phenomena, it is clear that four main stages of the South American episode can be recognized:

(1) The span between the extinction of the last Gondwanan land mammals and the very first immigration of the Laurasian Marsupialia and Placentalia (in part contemporaneous) as well as the late Eocene–early Oligocene immigration to South America of primates and rodents (apparently from Africa; Fig. 10). This interval corresponds to what we have distinguished as the "most autochthonous part of the history" (Pascual et al., 1985: 230–231; Figs. 9, 10), during which the basic diversification of the South American mammals occurred. This event also comprised the Protocenozoic and Infracenozoic Supercycles, which probably extended back to include the last part of the long Patagonian sterile Maastrichtian–earliest Danian span.

(2) The end of the Infracenozoic Supercycle led to the beginning of a new evolutionary cycle, marked by the late Eocene–early Oligocene Turnover (also known as La Grande Coupure or the Terminal Eocene Event). The archaic lineages of ungulate mammals (brachydonts) that had gradually changed from protohypsodont (Eopatagonian Cycle) to almost eu-

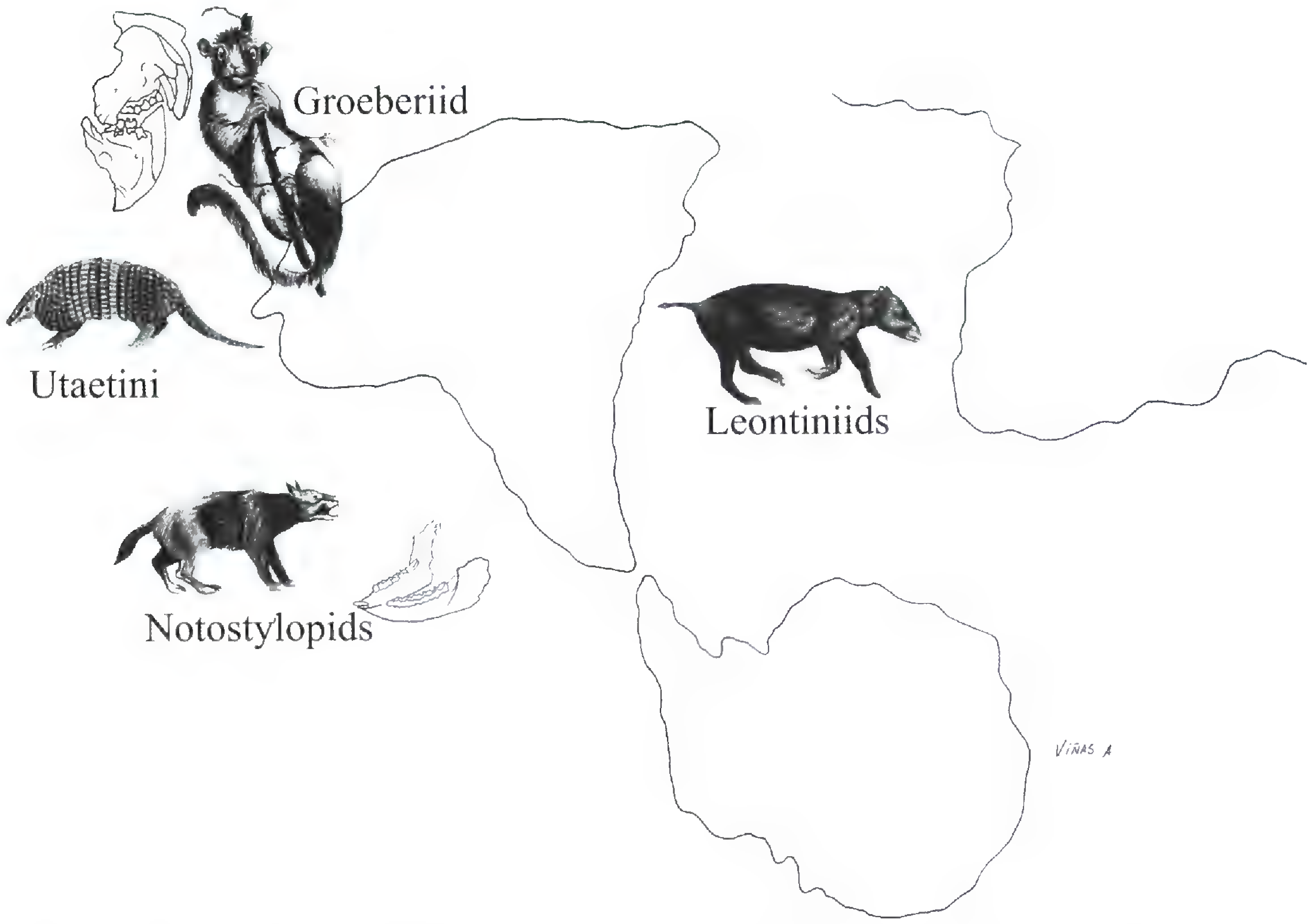


Figure 9. By the late Eocene (ca. 30 mybP) the South American continent was isolated. During the Eocene, the immigrant Therians had differentiated into the most advanced and varied lineages of mammals, e.g., the marsupial Groeberiid, the xenarthran dasypodids, Utaetini, and the notoungulates, Notostylopids, and Leontiniids. We recognized this interval as the most autochthonous part of the South American mammalian history.

hypsodont types (sensu Mones, 1979, 1982) (Prepatagonian Cycle), was replaced by a quite modern stamp of native ungulates (euhypsodont), which characterized most of the native ungulates of the Patagonian Cycle and all subsequent cycles up to the end of the Pleistocene (Panaraucanian and Pampampean Cycles; Table 1). We qualified the beginning of this process (i.e., the Patagonian Cycle) as "The First Major Change Toward a Modernization" (Pascual et al., 1985: 232–234). At this point, the history of South American mammals passed from "Early Experimentation to Modern Standardization" (*fide* Gould, 1983: 21). This turnover appears to be regionally connected to climatic and/or environmental changes, related to a series of geotectonic phenomena, e.g., the diastrophic Inca Phase, and quite possibly also the Pehuenche Phase (see Tertiary Andine Diastrophism in Table 1), the completion of the Drake Passage, and the consequent separation of South America from Antarctica as an island continent (Fig. 10), with all the climatic consequences derived from the formation of the encircling Antarctic Current.

Thus, the evolutionary processes leading to the differentiation of the unique South American land mammals, until ca. 30 mybP, also had the Antarctic Peninsula, and probably some other portion of the Antarctic continent, as substratum. Simpson's (1950) Ancient Immigrants developed on this scenery. Simpson's two other episodes (Faunal Strata in a figurative sense), which he named Old Island Hoppers and Late (Island Hoppers and) Immigrants (Simpson, 1950: 364), respectively, developed while the continent was isolated, except toward the end when the inter-American terrestrial connection began with the newborn Panamanian Land Bridge (ca. 2.5 mybP), and through it the terrestrial transit (i.e., walking) of what Stehlin and Webb (1985) termed The Great American Biotic Interchange. During the isolation period preceding this interchange the modernization of the native mammals increased, particularly manifested in the augmentation of hypsodontism of the herbivore grazers among the native placental mammals, as well as in some peculiar marsupials, such as the Argyrolagidae (*Proargyrolagus* Wolff) and the Patagoniidae (*Patagonia* Pascual and Carlini). Two main subcycles characterize this interval (Pascual et al., 1985): the Deseadan Subcycle and the Pan-Santacrucian Subcycle.

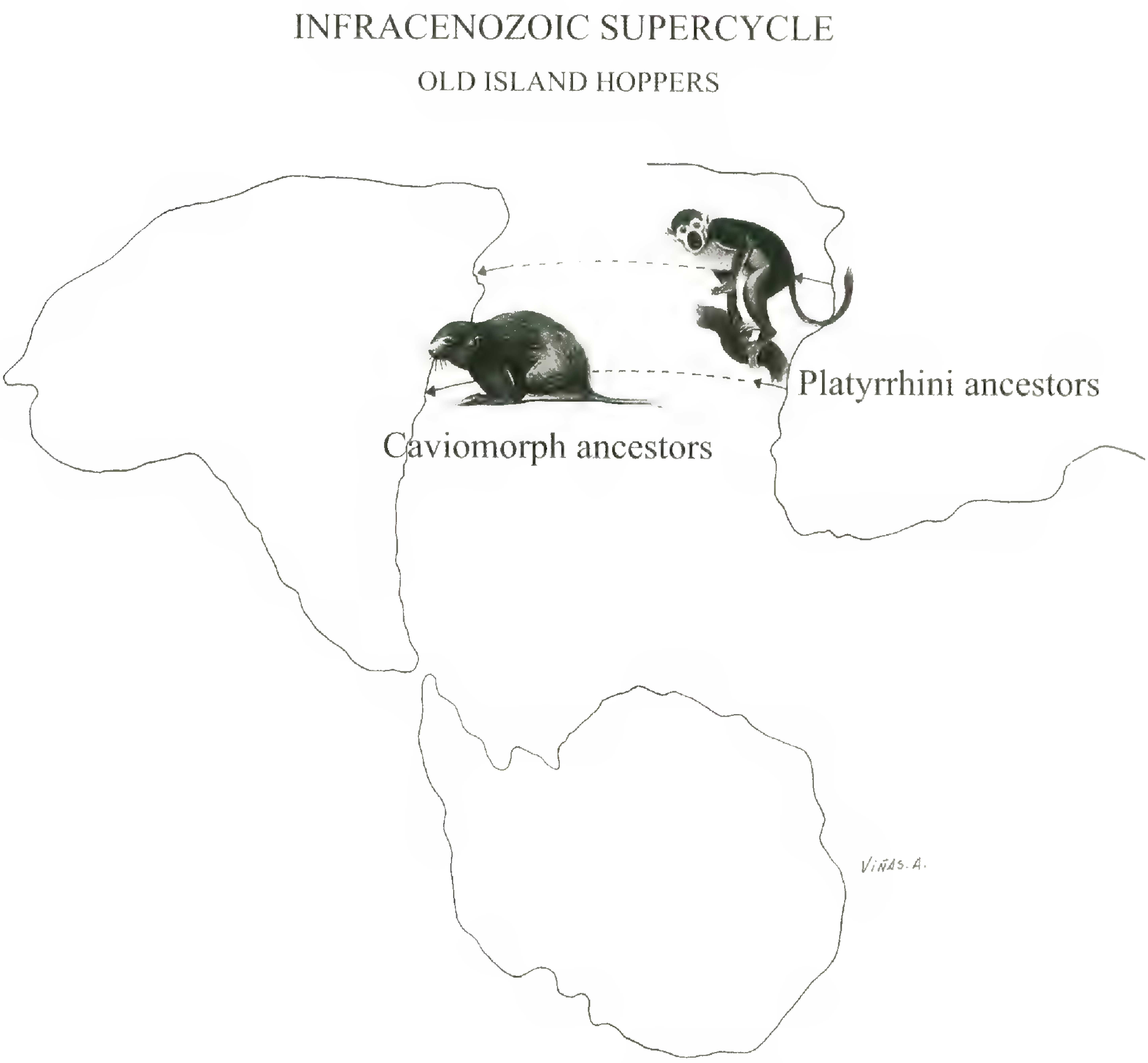


Figure 10. Approximately coincident with the separation of the South American and Antarctic continents (ca. 30 mybP), rodents (non-cricetids) and primates immigrated from Africa by sea.

During the Deseadan Subcycle (late Oligocene–earliest Miocene), according to the Patagonian record, over the southern extreme of the continent the most primitive Paleogene mammals vanished or disappeared and some very important cladogenetic processes came to an end, especially within very diverse lineages. On the other hand, from small contemporaneous mammals related to the latter, new cladogenetic processes began. For example, certain notoungulates evinced the precocious acquisition of high-crowned teeth, and caviomorph rodents were recorded for the first time at austral latitudes (see Patterson & Pascual, 1972; Pascual et al., 1985, and literature therein). According to Zachos et al. (2001), this cycle occurred between two glaciations, known as Glaciation Oi-1 and Glaciation Mi-1, which developed in Antarctica and the southernmost part of the South American continent. Furthermore, also according to Zachos et al. (2001), completion of the Drake Passage occurred in between these two glaciations (Table 1), i.e., around 30 mybP.

The following Pan-Santacrucian Subcycle represents the southernmost record of any of the South American SALMAs. Apparently related to the end of the Mi-1 Glaciation, a change to relatively mild conditions occurred. These mild conditions culminated about 15 mybP, with the so-called Mid-Miocene Climatic Optimum, and correspond to the time that preceded the Quechua Phase of the Tertiary Andean Diastrophism. Considering the entire fauna, Webb (1978) remarked that its rich diversity of medium to large-sized mammals strongly infers a broad environmental impact, i.e., an optimum balance between grasslands and woodlands provided by savanna. An intense drop in sea level ca. 30 mybP occurred due to glaciation, followed by intermittent drops in sea levels culminating with the Plio–Pleistocene glaciations (Table 1). Around 18 mybP the first emigration of native South American land mammals occurred, although not to North America but to the West Indies. Around that time, caviomorph rodents and megalonychid xenarthrans (Fig. 11) and probably also the

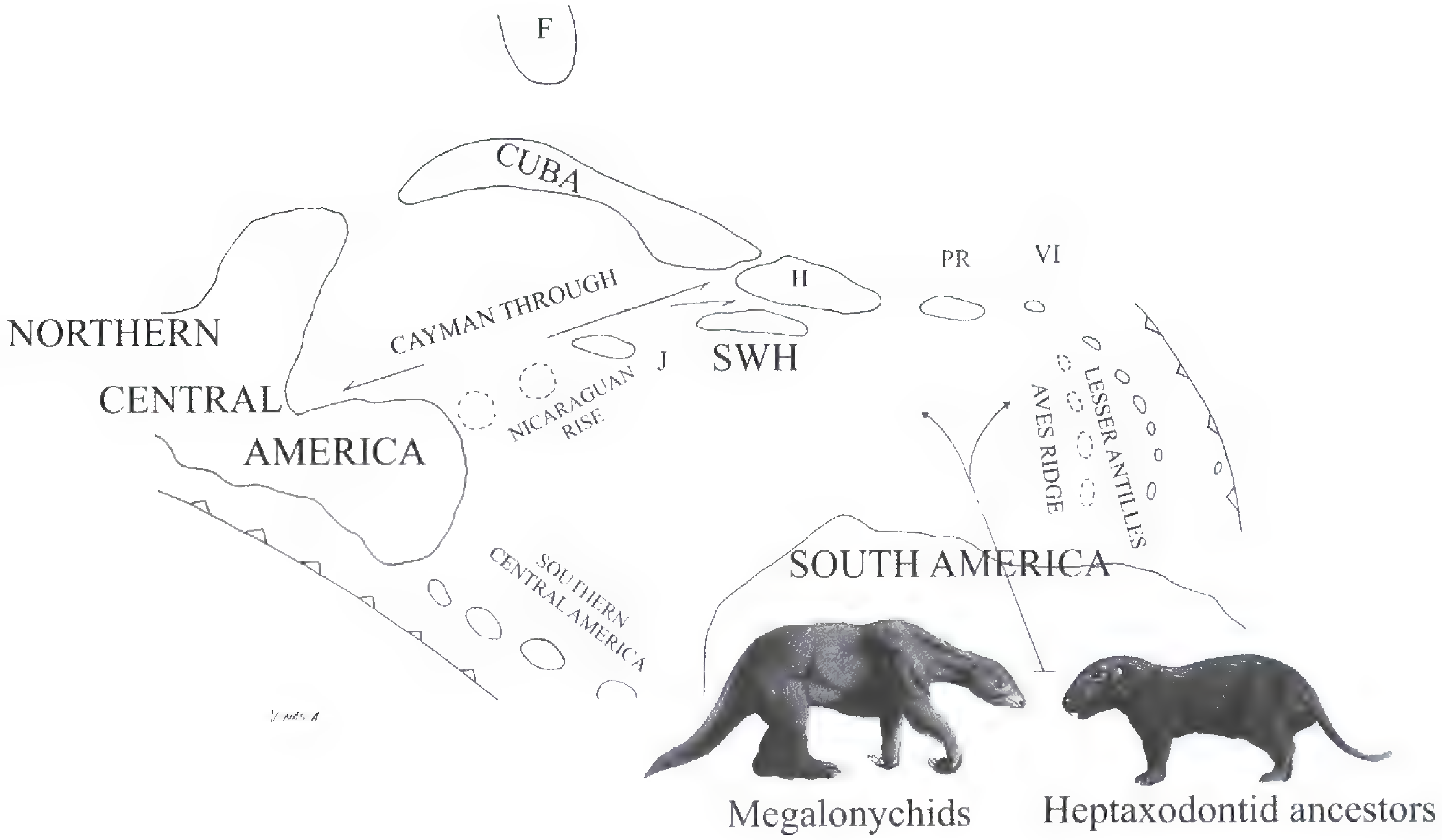


Figure 11. By 18 mybP the first dispersal event of South American mammals occurred: Xenarthran Megalonychids and Dinomyid rodents emigrated (as island-hoppers) to the West Indies.

platyrrhine primates—populated the Antilles, most likely as island-hoppers. There they underwent a notable evolutionary radiation. The megalonychid xenarthrans, the heptaxodontid rodents, and the platyrrhine primates became extinct quite recently, within historical times, while the capromyid rodents are extant. These are regional descendants of those South American immigrants, or probable vicariant taxa according to MacPhee & Iturralde-Vinent (1994). Curiously, both the megalonychid xenarthran and the heptaxodontid rodents differentiated into some peculiar ecological types, including tree-sloth-like forms (Matthew & Paula Couto, 1959; Paula Couto, 1967; Pascual et al., 1990) and cursorial, elasmodont heptaxodontid rodents very similar to the Miocene South American phoberomyine neoepiblemids and eumegamyine dinomyids (Pascual et al., 1990). Among the West Indies rodents, all those with elasmodont molariform dentition have been lumped into a single family, Heptaxodontidae, although sometimes with hesitation (e.g., Ray, 1964). Nevertheless it is suggestive that the peculiar Jamaican *Clidomys* Anthony, 1920 (see MacPhee et al., 1983; MacPhee, 1984) is very similar to the South American Neoepiblemidae in dental structure. On the other hand, the remaining Heptaxodontidae are more similar to the highly diversified Dinomyidae. This difference may indicate that there was more than one immigratory event of rodents (Fig. 11).

The following Pan-Araucanian Cycle, as we called it (Pascual et al., 1985), was with the diastrophic Quechua Phase, known by most geologists as the orographic phase (e.g., Vicente, 1972). The elevation of the Andes displaced the most propitious environments for land mammals to both sides of the cordillera (Ortiz-Jaureguizar et al., 1993). On the eastern sector of the rising Andes, extensive plains arose, first comprised of pyroclastic mammal-bearing sediments, and then clastic sediments; the middle pampas region also had an important component of pyroclastic sediments.

Mammals on opposite sides of the cordillera had long been considered as representing two distinct and successive ages (e.g., Marshall & Salinas, 1990). On the basis of a multivariate analysis, Ortiz-Jaureguizar et al. (1993) suggested that they are correlative and proposed that both be maintained under the original name of the Friasian SALMA. The Frias Formation, both in Patagonia and in extra-Patagonian regions of Argentina, was deposited under the influence of the withdrawal of an extensive middle Miocene marine transgression. We (Pascual et al., 1996: 291) made the interpretation that the distinction of the Friasian land mammals with respect to the preceding subtropical Santacrucian one was related to the climatic and environmental effects of the first subphase of the complex Quechua orographic phase, as well as to the global climatic changes, as evidenced by the

relatively sudden divergence between high and low latitude marine temperatures. According to Savin and Stehli (1975), high-latitude temperatures dropped dramatically, but low-latitude temperatures remained constant or even perhaps increased. In a period probably not exceeding 2 to 3 million years, minimum temperatures appear to have dropped 3°C, or at a rate of about 1°C per My. Based on fossil land mammals and other tetrapods, the wide-ranging plains that built up on the eastern slopes of the Andes became successively more and more arid to the west, with more humid portions to the northeast influenced by the humid Atlantic winds. The successive sedimentologic mammal-bearing units deposited toward the northeast part of Patagonia (Chasicoan, Huayquerian, Montehermosan, and Chapadmalalan SALMAs) progressively contain a notable increase in North American immigrants corresponding with a change toward finest granulometric sediments (silty–loessoid), as well as with the pace that the Panamanian land bridge was being built up.

Contrary to the increasing trend of eupsydontism in the native ungulates, the immigrant ungulates were brachydont, or at the most mesodont. The withdrawal of the Miocene marine transgression was succeeded by a period of similarly widespread and varied plains that we distinguished as the "edad de las planicies australes" (Pascual & Bondesio, 1982: 29). In such a way the late Miocene–Pleistocene pampas of present times initiated their differentiation. Mammal-bearing sediments, with good ecological indicators, clearly show the north-northeast environmental displacement. At the beginning, i.e., during the middle Miocene, the last appearances of some Santacrucian mammals are recorded (Pascual et al., 1965: 177). In general, and in accordance with the

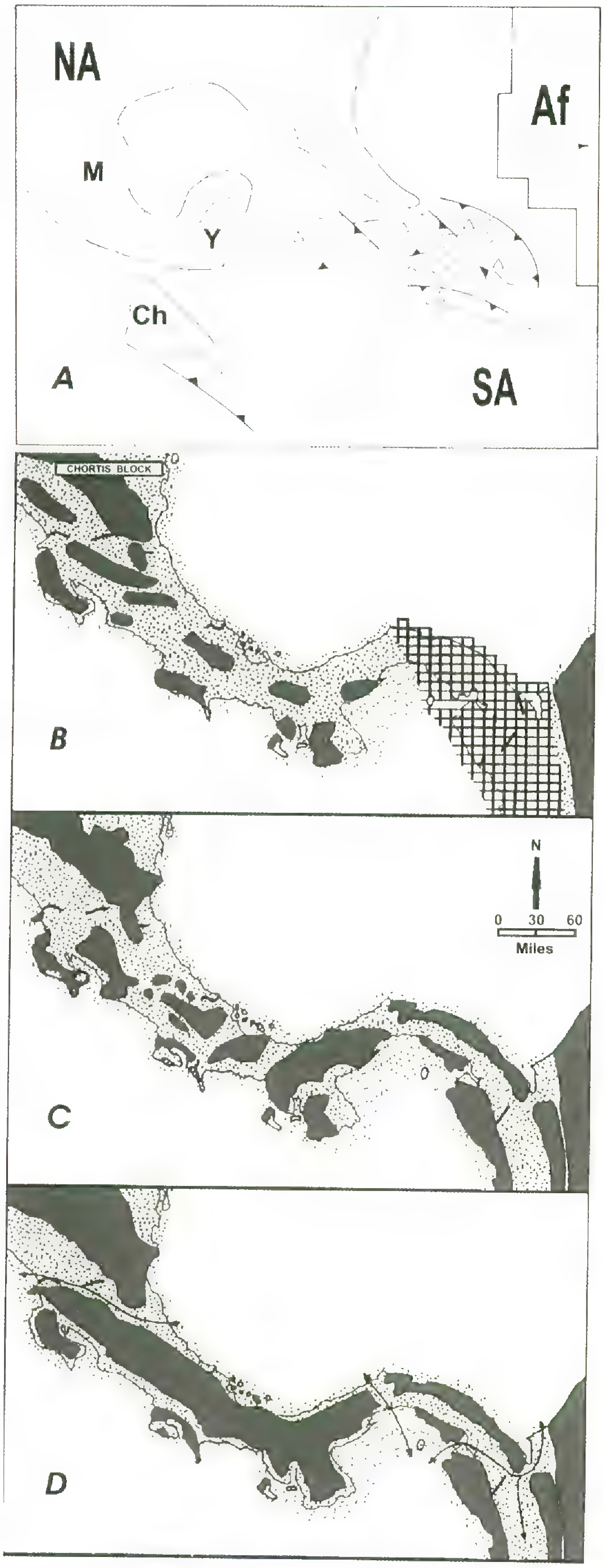


Figure 12. The rising Panamanian land bridge established a definitive connection between North and South America. —**A.** By 85 mybP the interamerican "exchange" of terrestrial tetrapods began: hadrosaur dinosaurs from North America and titanosaur saltasaurines from South America. Apparently this occurred through some kind of land bridge (archipelagic) related to Donnelly's (1973, 1985) Flood Basalt Episode. **M** = Mexican block; **Y** = Yucatán block; **Ch** = Chortis block. (A modified from Donnelly, 1985, with permission of Springer Science and Business Media.) —**B.** About 15–16 mybP, the present Panamanian Land Bridge was occupied by an abyssal sea more than 2000 meters deep. —**C.** Some time before 7 mybP the Caribbean region began to be built up and the "Island Hoppers" interchange (Simpson, 1950) began. —**D.** Between 2.5 and 3 mybP the terrestrial inter-American connection was almost completed and, consequently, the formation of the present American Atlantic coast was also almost complete. This, and the subsequent final connection, began the massive interchange of terrestrial mammals, i.e., Simpson's "Late (Island Hoppers and) Immigrants." (A. Dotted lines indicate the present geographical limits; open triangles: calc-alkaline volcanism; closed triangles: subduction and island-arc or continental-margin magmatism around the Caribbean. B–D. Grey shading: continental blocks; dotted areas: shallow marine environments; grids: deep marine (> 2000 m) environments. D. Lines with arrows: seaway.) (B, C, and D reprinted from *Paseo Pantera: Una Historia de la Naturaleza y Cultura de Centroamerica* by Anthony G. Coates (Washington, DC: Smithsonian Books). Used by permission of the Smithsonian Institution. Copyright 2003.)

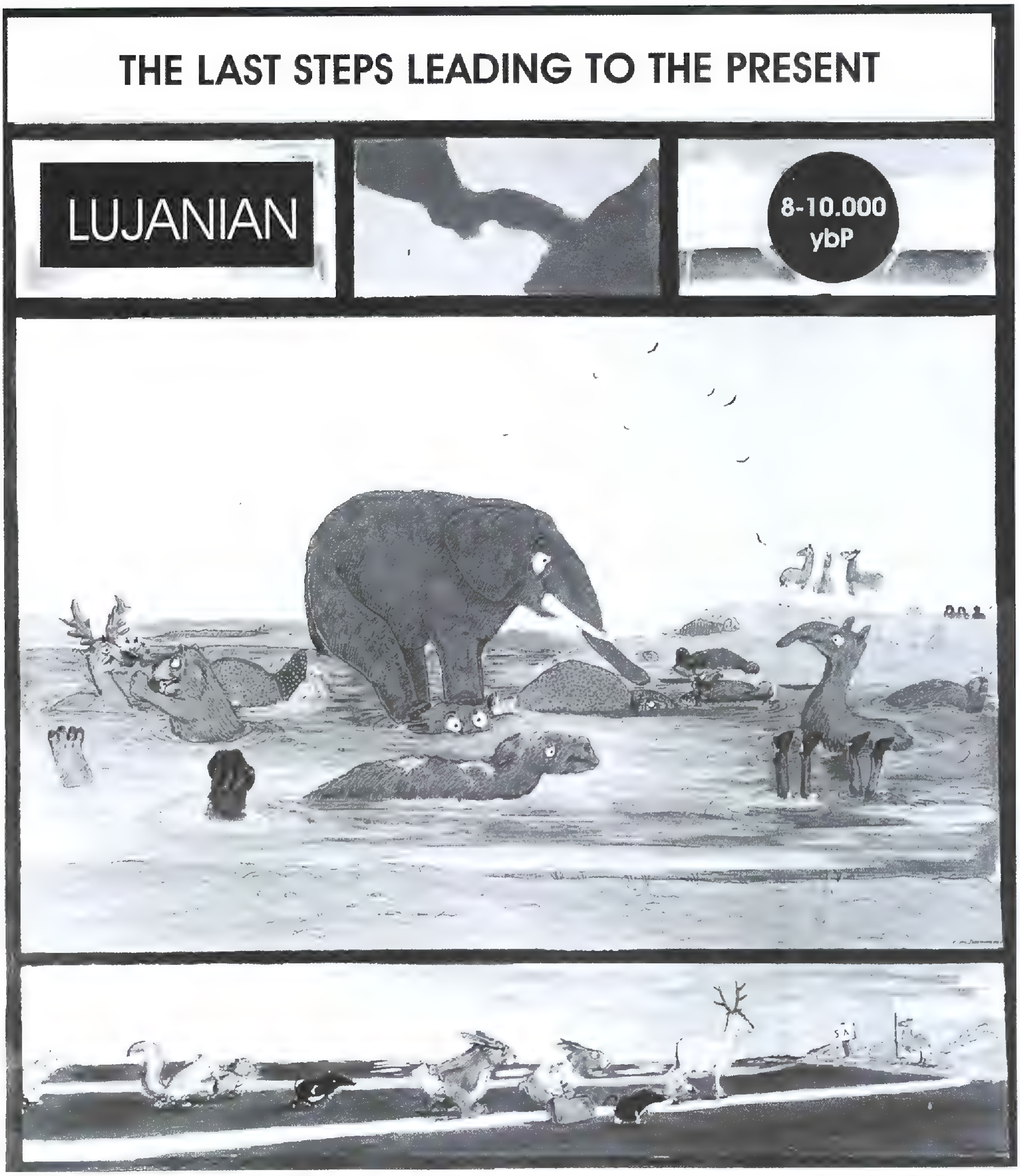


Figure 13. About 8000–10,000 ybP the "Megafaunal Extinction" and subsequent newcomers began to feature in the modern Neotropical mammal assemblage.

fossil record, the abundance of native ungulate herbivores was markedly reduced, accompanied by a great increase in the numbers of such specialized herbivores as huge edentates and caviomorph rodents. It is important to emphasize that there was a successive gradual increase in immigrants of North American origin toward the end of the Miocene, from the Late Island-hoppers to the early walkers, through the rising Panamanian Bridge, i.e., Simpson's (1950) Late (Island Hoppers and) Immigrants (cf. Fig. 12 B–D). Within the temperate regions of the continent, forest progressively declined and was replaced by extensive grasslands. As a consequence, cursorial and grazing native communities of mammals spread, setting the stage for the forerunners of the pampean's (late Pliocene–Pleistocene) peculiar inhabitants.

(3) The third stage is marked by the beginning of the interamerican exchange of land mammals, which prima facie is related to the beginning of the land connection between the Americas, in part due to the sustained low sea level that followed the Quechua Phase (Table 1, Eustatic Curve). As a consequence, a notable increase of North American immigrants occurred; the supposedly strong influence of these immigrants on the extinction of native mammals has been strongly disputed (e.g., Patterson & Pascual,

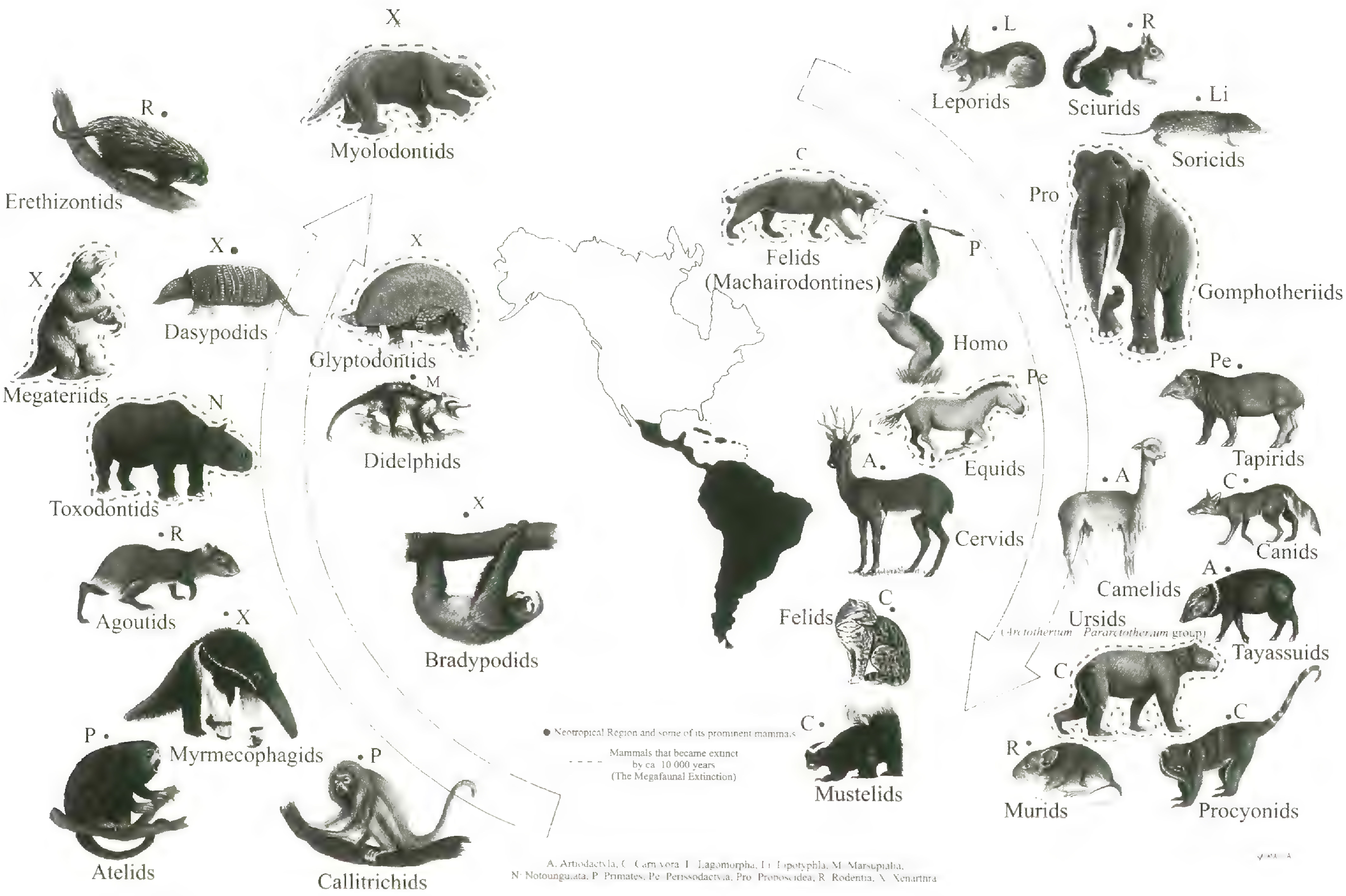


Figure 11. Between 2.5 and 3 mybP the principal interchange of the Great American Biotic Interchange (Stehli & Webb, 1985), whose acme was about 1.5 mybP, began. "The predominance of savanna-adapted mammals indicates a continuous corridor of such vegetational formations as thorn scrub or seasonally arid woodland, whereas they are now separated by at least 1700 km of humid tropical forest. . . The final link between American mesic equatorial biotas evidently was established in the late Pleistocene" (Webb, 1985: 381). The fates of mammals that participated in the Great American Biotic Interchange, up to the present Neotropical Region, are indicated on each of the most representative selected taxa depicted here.

1972; Cifelli, 1985). During the 5th International Theriological Congress in Rome (1989), Ortiz-Jaureguizar (1989: 277–278), Goin (1989: 271–272), and Tonni et al. (1989: 285–286), among others, again questioned the competitive model for extinction of the South American latest Pleistocene mammals.

There is hard evidence that some South American megalonychid and mylodontid xenarthrans (Webb's (1985: 358–359) "heralds of the South"), and apparently some North American carnivores such as the procyonids, were able to cross the marine barriers from about 8 to about 9 mybP, i.e., more than 5 Ma before the completion of the Panamanian land bridge, estimated at 2.5–3 mybP (Fig. 12). These taxa were among Simpson's Late Island Hoppers. Thus, the final terrestrial connection of the Americas by the newly built Panamanian bridge initiated the massive inter-american exchange, whose acme occurred by the Ensenadan SALMA, between 1.8 mybP and ca. 60,000 ybP (Cione & Tonni, 1995, 2001). This occurred concomitantly with a progressive extinction of most of the native mammals, culminating in what has been called "The Megafaunal Extinction" by Martin (1984: 355; see figures encircled on Fig. 14), which was an extinction phenomenon that, with some temporal differences, occurred almost all over the world.

(4) The last and fourth stage that marks the history of South American mammals is the so-called "Megafaunal Extinction" (Fig. 13). This is an extraordinary event that took place about 10,000 years ago. Together with the preceding arrival of man about 13,000 years ago, this event shaped the basic mammalian fauna of the present Neotropical Region (see representative taxa with bullets in Fig. 14). Simultaneously or somewhat later, i.e., in post-Pleistocene times, the last North American immigrants (quite probably inhabitants of Central America) arrived. These included rodents such as Heteromyidae, Geomyidae, and Sciuridae; Lagomorpha such as Leporidae; and Insectivora such as Soricidae. Also included were some genera of families already living in South America, such as the cervid *Odocoileus* Rafinesque (see the lower part of Fig. 13).[3]

[3] Exhaustive details related to the integrated geobiotic phenomena that led to The Great American Biotic Interchange can be found not only in this Symposium, particularly in the paper by S. D. Webb, but also in the 1985 book *The Great American Biotic Interchange*, Stehli and Webb (editors); *Late Cenozoic Mammals*, Symposium 9 of the 5th International Theriological Congress in Rome, R. Pascual and S. D. Webb (editors), 5th ITC, Rome, 1989, Abstract of Papers and Posters, Vol. 1, pp. 260–291; Chapters 1, 2, 4, and 5 of the 2003 book *Paseo Pantera: Una Historia de la Naturaleza y Cultura de Centroamérica*, A. G. Coates (editor), Smithsonian Institution Press, Washington D.C. and London; the 1996 book *Evolution and Environment in Tropical America*, J. B. C. Jackson, A. F. Budd, and A. G. Coates (editors), The University of Chicago Press; and the 1999 book *A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama*, L. S. Collins and A. G. Coates (editors), Bull. Amer. Paleontol. 357.

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PALEOGEOGRAPHY OF THE ANTILLES AND ORIGIN OF WEST INDIAN TERRESTRIAL VERTEBRATES[1]

S. Blair Hedges[2]

Abstract

The fauna of the West Indies includes more than 1300 native terrestrial vertebrate species and is characterized by high levels of endemism. Several theories have been proposed to explain how these animals arrived to the islands, including dispersal, vicariance, and land bridges. The dispersal theory proposes that most of the West Indian terrestrial biota arrived by flying or by flotsam. The vicariance theory suggests that there was a proto-Antillean land mass, or masses, connecting North and South America in the late Cretaceous that traveled eastward as the Caribbean geologic plate developed and carried an ancient biota with it. One widely discussed land bridge theory proposes that much of the Antillean biota originated by dispersal over an unbroken dry land connection, the Aves Ridge, between South America and the Greater Antilles 35–33 Ma. Geologic evidence cannot unambiguously support or refute any of these models, despite claims to the contrary. Other evidence bearing on these three theories, or mechanisms, comes from the taxonomic composition of the fauna, their phylogenetic relationships, fossil record, paleogeography, ecology, climate, water currents, and divergence time estimates from molecular clocks. This evidence supports an origin by overwater dispersal for most or all of the West Indian terrestrial vertebrate fauna. The strongest support comes from a reduced higher-level taxonomic composition of the fauna (now and in the past), the presence of unusually large adaptive radiations, and the finding of divergence time estimates between island and mainland groups that are not clustered around a particular time. In addition, the majority of terrestrial (non-flying) groups have closest relatives in South America, which is consistent with the direction of water currents and most hurricane tracks. Some of the same evidence in support of dispersal argues against a mid-Cenozoic land bridge from South America. Several ancient, relictual groups (e.g., xantusiid lizards and solenodontoid shrews) may have arisen through proto-Antillean vicariance, and molecular clock analyses—here revisited—provide support for this, but an origin by dispersal can also be argued. No model can be completely discounted. Although the general pattern (dispersal) has emerged, many details remain to be determined concerning the origin of the fauna.

Keywords: animals, biogeography, Caribbean, dispersal, systematics, vertebrates, vicariance, West Indies.

Resumen

La fauna de las Antillas incluye más de 1300 especies nativas de vertebrados terrestres y se caracteriza por altos niveles de endemismo. Se han propuesto varias teorías para explicar cómo estos animales llegaron a las islas, incluyendo dispersión, vicarianza, y corredores terrestres. La teoría de la dispersión propone que la mayoría de la biota terrestre antillana llegó volando o en restos flotantes. La teoría vicariante sugiere que hubo una masa (o masas) de tierra proto-antillana, que conectaba a América del Norte y del Sur en el Cretácico tardío y que se desplazaba hacia el este mientras la placa geológica del Caribe se desarrollaba y llevaba consigo una biota antigua. Una teoría ampliamente discutida acerca del corredor terrestre propone que la mayoría de la biota antillana se originó por dispersión sobre una conexión seca intacta de tierra, el Promontorio de Aves, entre América del Sur y las Antillas Mayores hace 35–33 Ma. La evidencia geológica no puede apoyar o refutar en forma inequívoca cualquiera de estos modelos, a pesar de que se opine lo contrario. Otra evidencia concerniente a estas tres teorías, o mecanismos, proviene de la composición taxonómica de la fauna, de sus relaciones filogenéticas, del registro fósil, de la paleogeografía, la ecología, el clima, las corrientes de agua, y estimados de tiempo divergentes de los relojes moleculares. Esta evidencia apoya un origen por dispersión para la mayoría de la fauna vertebrada terrestre antillana. El apoyo más fuerte proviene de una reducida composición taxonómica de alto nivel de la fauna (en el presente y el pasado), la presencia de radiaciones adaptativas inusualmente grandes y el hallazgo de divergencia en los estimados de tiempo entre grupos de las islas y del continente que no se agrupan alrededor de un tiempo particular. Además, la mayoría de grupos terrestres (que no vuelan) tienen parientes más cercanos en América del Sur, que es consistente con la dirección de las corrientes de agua y de la mayoría de huracanes. Algunas de las mismas evidencias de apoyo a la dispersión argumentan en contra de un corredor terrestre desde América del Sur en el Cenozoico medio. Varios grupos antiguos, relictos (e.g., lagartos xantusiidos y musarañas solenodontoides) pudieron haber surgido a través de vicarianza proto-antillana, y los análisis de relojes moleculares—aquí revistos—dan apoyo a esto, pero también se puede argüir un origen por dispersión. Ningún modelo se puede descartar totalmente. Aunque el patrón general (dispersión) ha sobresalido, todavía quedan por determinar muchos detalles referentes al origen de la fauna.

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Table 1. Taxonomic diversity of native West Indian terrestrial vertebrates.

Group	Orders	Families[a]	Genera			Species		
			Total	Endemic	% Endemic	Total	Endemic	% Endemic
Freshwater fishes	6	9	14	6	43	74	71	96
Amphibians	1	4	6	1	17	173	171	99
Reptiles	3	19	50	9	18	499	478	96
Birds	15	49	204	38	19	425	150	35
Mammals:								
Bats	1	7	32	8	25	58	29	50
Other[b]	4	9	36	33	92	90	90	100
TOTALS	30	97	342	95	28	1319	989	75

[a] Includes one endemic family of birds (Todidae) and four of mammals (Capromyidae, Heptaxodontidae, Nesophontidae, and Solenodontidae).
[b] Edentates, insectivores, primates, and rodents.

The West Indies has captured the attention of biogeographers for over a century (Wallace, 1881). Some of the reasons for this include a large but taxonomically peculiar fauna, high levels of endemism, and an intriguing physiography. For example, there are four large islands, the Greater Antilles, now known to be quite old (ca. 100 million years); a large group of smaller, flat islands on a limestone plateau, the Bahamas Bank; and a textbook-like arc of volcanic islands, the Lesser Antilles. When plate tectonics and past sea-level fluctuations are added, this physical setting presents a complex challenge for the biogeographer. The primary task is to understand how and when the biota arrived. A comprehensive review of Caribbean biogeography is not possible in this limited space, and thus for additional insights see recent reviews by Hedges (1996a, c, 2001), Iturralde-Vinent & MacPhee (1999), Graham (2003a, b), and Santiago-Valentin and Olmstead (2004), some of which will be discussed and contrasted herein. Although models of historical biogeography apply to both plants and animals, examples will be drawn from the latter, and primarily land vertebrates of the West Indies.

Most groups of West Indian invertebrates are poorly known. Examples of some groups that have been given taxonomic attention are ants (Wilson, 1985, 1988; Morrison, 1998), termites (Scheffrahn et al., 2003), butterflies (Smith et al., 1994), earthworms (James, 1996), land snails (Gould & Woodruff, 1986; Goodfriend & Gould, 1996), scorpions (deArmas, 1982), mites (Niedbala, 2004), and selected other groups (Liebherr, 1988, 1992). Fossils from Dominican amber have added significantly to the knowledge of West Indian invertebrate diversity. In some cases the amount of information is so detailed and material of such high quality that complex ecological and behavioral interactions can be inferred (Poinar & Poinar, 1999). However, studying the historical biogeography of a group is difficult when a majority of the living species has yet to be discovered. West Indian vertebrates, on the other hand, are better known taxonomically, and therefore most zoogeographic analyses have focused on these animals.

Currently 1319 species of living vertebrates are known from the West Indies (Table 1). Relatively few new species of mammals and birds are being encountered, indicating that knowledge of the species diversity of those two groups is nearly complete. However, amphibians, reptiles, and to a lesser degree freshwater fishes, show more steeply rising discovery curves, suggesting that undescribed species still exist (Hedges, 1996a, c). Amphibians (173 species), reptiles (499 species), and birds (425 species) are the most species-rich groups, although levels of endemicity differ considerably. Only about one-third of bird species (35%) are endemic to the West Indies, whereas nearly all species of amphibians (99%), reptiles (96%), and freshwater fishes (96%) are endemic. That the ability to fly is the reason for this difference is seen clearly in mammals; only 50% of bats are endemic, whereas all non-flying mammals are endemic (Table 1).

Not unexpectedly, most West Indian vertebrate fossils are from the Quaternary, <1.8 million years ago (Ma), and most often are from regurgitated remains of owl meals and victims of natural pitfalls (Pregill & Olson, 1981; Pregill, 1986; Pregill et al., 1992). Approximately 15 to 20 vertebrate taxa are known from the Paleogene (65–1.8 Ma), including those in amber (MacPhee & Iturralde-Vinent, 1994, 1995; MacPhee & Grimaldi, 1996; Poinar & Poinar, 1999). The amber fossils are mostly from the same formation, but the date (30–15 Ma) has been disputed (Grimaldi, 1995; Hedges, 1996a; Iturralde-Vinent & MacPhee, 1996). With such a small number of Paleogene fossils, a clear picture of the Paleogene

vertebrate fauna is not available. However, current fossils suggest that the fauna was similar to the Quaternary fauna in higher-level taxonomic composition. For example, fossils of frogs (*Eleutherodactylus* Dumeril & Bibron), lizards (*Anolis* Daudin and *Sphaerodactylus* Wagler), a snake (*Typhlops* Oppel), and a mammal (Solenodontidae) are representatives of vertebrate groups present today on the islands (MacPhee & Grimaldi, 1996; Poinar & Poinar, 1999). Giant megalonychid ground sloths (Order Edentata) underwent a major adaptive radiation in the Antilles, as evidenced from Quaternary fossils, and their fossils are known starting from the Early Oligocene, ca. 33 Ma (MacPhee & Iturralde-Vinent, 1995). Primates are also known from the Paleogene and Quaternary of the West Indies (MacPhee & Iturralde-Vinent, 1995; MacPhee & Horovitz, 2004). No sloths or native primates occur in the West Indies today. A rhinoceros relative (*Hyrachyus* Leidy) is known from the Eocene (ca. 50 Ma) of Jamaica (Domning et al., 1997), but no other ungulates are known from the West Indies subsequent to that record. In fact, *Hyrachyus* may represent a survivor of the proto-Antilles or an early disperser from Central America (Domning et al., 1997; Pregill, 1999; Hedges, 2001).

Although many naturalists have commented on the West Indian fauna over the centuries (e.g., Sloane, 1725; Gosse, 1851; Darwin, 1859), Wallace (1881) was one of the first to discuss the historical zoogeography of the islands. He noticed that the higher-level taxonomic composition of the West Indian fauna was reduced when compared to that of mainland areas, a fact also noted by subsequent zoogeographers (Matthew, 1918; Simpson, 1956; Darlington, 1957; Williams, 1989). Such patterns are characteristic of oceanic islands where the fauna has arrived by dispersal, rather than of islands previously connected to mainland areas (Williams, 1989; Paulay, 1994). However, much of the debate during the first half of the 20th Century concerned the possibility of land bridges (Scharff, 1912; Barbour, 1916; Schuchert, 1935). Since about 1960, knowledge of seafloor topography and the acceptance of plate tectonics have greatly changed the physical backdrop for zoogeographic studies, and rendered the suggestions of those land bridges obsolete. For this reason, I briefly review the current knowledge of geology, water currents, and climate, before discussing contemporary models of Caribbean zoogeography.

Geologic History and Paleogeography

The Caribbean region was formed when the supercontinent Pangaea broke apart in the Jurassic (200–150 Ma). The initial ocean floor that was created by a spreading center has since been recycled through subduction. The current Caribbean Plate formed in the eastern Pacific in the mid-Cretaceous and has moved east-northeast relative to the American Plate (Dengo & Case, 1990; Donovan & Jackson, 1994; Pindell, 1994; Pindell & Kennan, 2002), although models that do not require high rates of plate movement have been proposed (Meschede & Frish, 1998). The present-day Greater Antilles were formed mostly from subduction, and resulting island-arc volcanism, of the North American Plate under the lighter Caribbean Plate during this eastward movement (Fig. 1). However, collision of this Antillean island arc with the Bahamas Platform in the early Paleogene caused subduction to stop and a fault zone and short spreading center (Cayman Trough) to form south of Cuba, thus fixing Cuba and eventually northern Hispaniola and Puerto Rico to the American Plate. Subduction continued along the leading (east) edge of the Caribbean Plate during the Cenozoic, always feeding an island arc on the overriding (Caribbean) plate. Initially the arc was the Aves Ridge (probably then a chain of islands), but later in the Cenozoic the expression of arc materials (andesitic volcanism) transferred slightly eastward to its present position as the Lesser Antilles. Among the Lesser Antilles, Barbados is an exception, being emergent Atlantic sea floor caused by the buckling of the Atlantic oceanic plate. The northern boundary of the

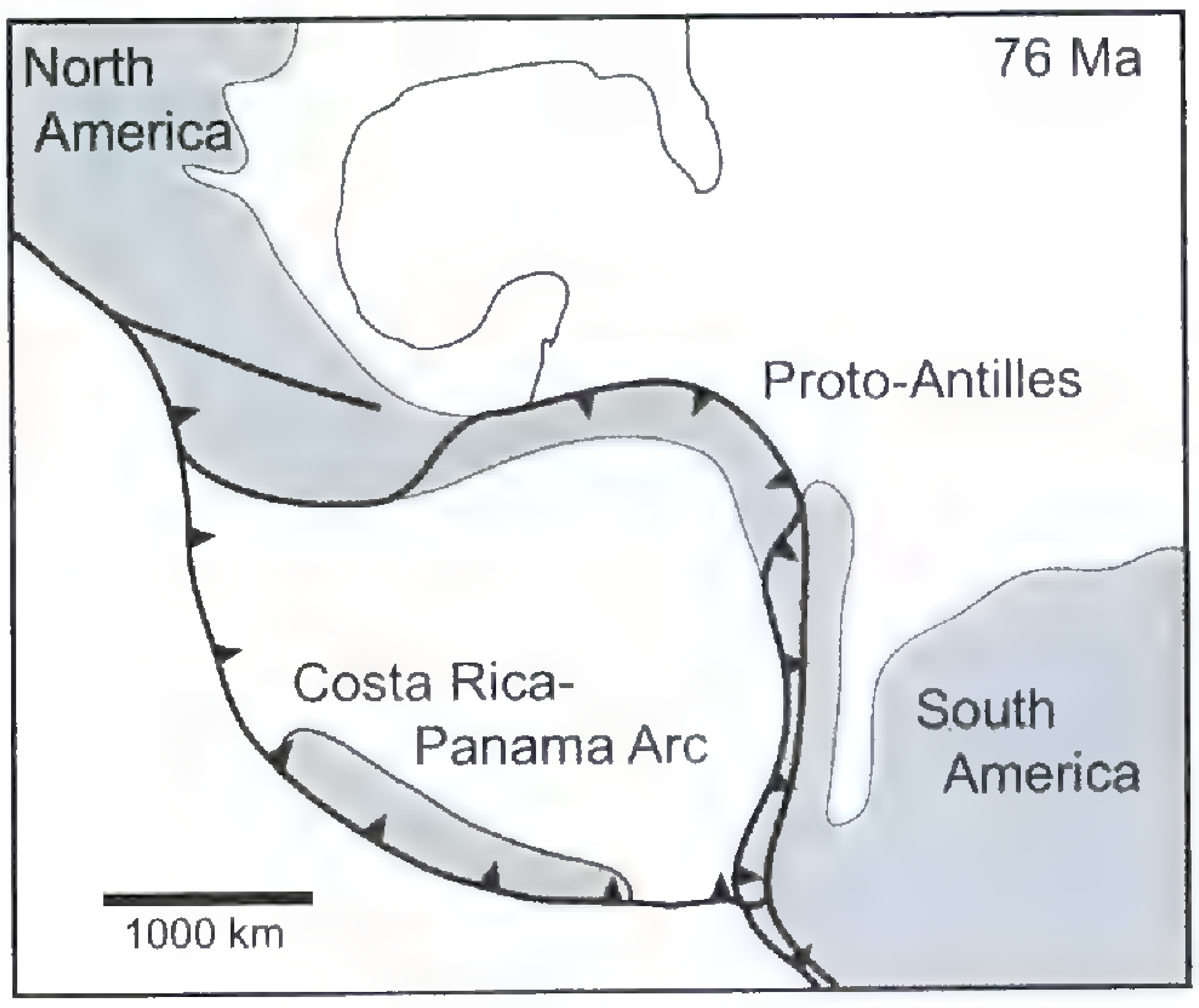

Figure 1. Location of the Proto-Antilles in the late Cretaceous (ca. 76 Ma), redrawn and modified with permission from Pindell (1994). Present coastline of southern North America is shown as narrow line; heavy lines without teeth are transform fault zones; heavy lines with teeth are subduction zones (teeth indicating direction of subduction). Shading denotes continental and arc areas that may or may not have been above sea level. This remains speculative for the Proto-Antilles, which may have been emergent, a chain of islands (as in the current Lesser Antilles), or completely submerged. The Costa Rica-Panama Arc is shown to the west.

plate has remained largely a transform fault and minor spreading center.

The Bahamas Platform has been a stable carbonate block on the North American Plate since the Cretaceous, and reef development has kept the platform near sea level apparently for much of that time. Although Jamaica and the southern portion of Hispaniola were initiated during the development of the proto-Antilles, their histories have been quite different from that of Cuba, northern Hispaniola, and Puerto Rico. They have been attached to the northern boundary of the Caribbean Plate and have moved eastward relative to Cuba and northern Hispaniola during the Paleogene. Jamaica has remained isolated during this time, but southern Hispaniola collided with northern Hispaniola in the Miocene (Huebeck & Mann, 1985), with the zone of attachment being the Cul de Sac-Valle de Neiba of present-day Hispaniola. The similar origin and proximity of Cuba, northern Hispaniola, and Puerto Rico raises the possibility that two, or all three, of these islands were attached at some point during the Paleogene, although that has yet to be firmly established (Pindell, 1994). The close similarity of the fauna of the Virgin Islands and Puerto Rico reflects the fact that they reside on the same bank. A more detailed account of Caribbean geologic history can be found elsewhere (Pindell, 1994; Pindell & Kennan, 2002).

Also of importance for biogeography is the paleogeography of the West Indies. This is a complicated problem because several poorly known variables must be considered simultaneously, such as sea level fluctuations, geologic uplift, and erosion. Some high mountain ranges (e.g., Blue Mountains of Jamaica) were uplifted over a period of only a few million years (late Miocene and Pliocene) and even higher ranges were eroded in less than a million years, as evidenced by the Eocene Wagwater Trough formation of Jamaica (Comer, 1974). Therefore, the current topography is a relatively poor guide of paleogeography during most of the Paleogene. Clearly, at some point between the inception of subduction in the mid-Cretaceous and today, the Antilles became emergent.

Determining when the islands first rose above the sea (and remained above sea level) and how, if at all, they were connected is not a simple task, and is often based on the distribution and type of marine sediments that presumably came from erosion of emergent areas. This type of information has suggested that the proto-Antillean island arc of the late Cretaceous probably was not a continuous (unbroken) land area resembling Central America but rather a chain of islands (Donnelly, 1989; Perfit & Williams, 1989; Donnelly, 1990, 1992; Pindell & Kennan, 2002), although the details are unknown. Some workers have claimed that no land areas in the Greater Antilles were constantly above sea level before 45 Ma (MacPhee & Iturralde-Vinent, 1994; MacPhee & Grimaldi, 1996; Iturralde-Vinent & MacPhee, 1999), although such absolute statements cannot be backed by existing evidence. To support this claim would require having an uninterrupted geologic record from most areas in the Caribbean region, and this is not yet available (Dengo & Case, 1990). In addition, small areas low in elevation would not be expected to yield large quantities of terrestrial sediments.

The claim by Iturralde-Vinent & MacPhee (1999) that no land areas in the Greater Antilles were constantly above sea level before 45 Ma, and their advocacy of a mid-Cenozoic dry land connection (Aves Ridge land bridge) with South America for the purpose of emplacing land mammals to the Antilles (see below), demonstrate that their models are not "paleogeography" but rather biogeography. The distinction is important because it provides the independence needed to falsify or test biogeographic models. For example, if a biogeographic model claims that animals must have walked across land to reach another area, and paleogeographic evidence says that no such land existed, then the biogeographic model can be rejected.

Finally, an important detail of Earth history of relevance to the Caribbean is the Cretaceous-Paleogene bolide impact of 65 Ma. This was one of the largest impacts in the inner solar system since the Precambrian, and is believed to have exterminated the dinosaurs and other groups (Hildebrand & Boynton, 1990). The impact site is in the Caribbean region under sediments of the Yucatan Peninsula (Kring & Boynton, 1992). At the time of impact, the islands of the Greater Antilles were only 1–3 crater diameters away (Pindell, 1994) and undoubtedly experienced massive waves hundreds to thousands of meters in height (Maurrassee, 1991). In addition to the global climatic effects of the impact, these local effects must have resulted in much extinction of the proto-Antillean fauna present on the islands at the time (Hedges et al., 1992).

Water Currents

The direction and speed of water currents is of importance to the dispersal of terrestrial organisms unable to fly. Even those non-piscine vertebrates capable of swimming are unlikely to swim against the current for long distances. For nearly all West Indian vertebrates, this mode of transport would involve rafting on floating vegetation (flotsam) washed into ocean currents from the mouths of rivers following

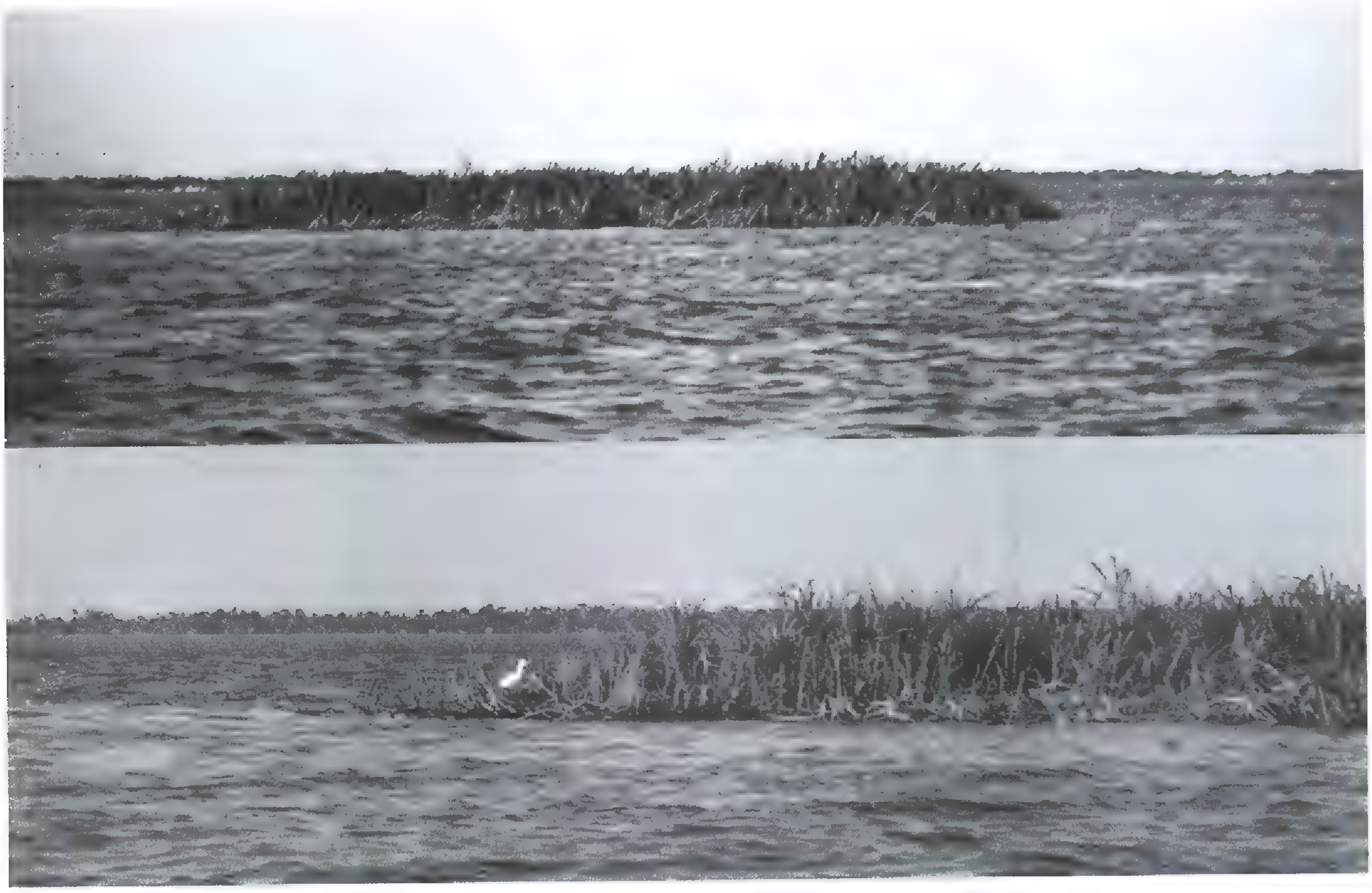

Figure 2. A floating island of vegetation (ca. 600 m²) near Santarém, Brazil, at the confluence of the Amazon and Tapajós rivers. The upper photo shows the entire island; the lower photo is a close-up of the left side, with a cattle egret (*Bubulcus ibis*), approximately 50 cm in height. Photograph taken by Pervaze Sheikh in February, 1997 (used with permission).

storms (Fig. 2). This method of dispersal is well known (Guppy, 1917; King, 1962; Heatwole & Levins, 1972), and has been documented for West Indian vertebrates (Henderson et al., 1995; Censky et al., 1998; Knapp, 2000).

In the West Indies, the present-day surface current flow is predominantly from the southeast to the northwest, and would have been similar in the past (Fig. 3). This is because the Caribbean is in the southwestern portion of the North Atlantic Gyre, the clockwise flow of water in the Atlantic. The clockwise flow is the result of the differential rotational velocity of the Earth (Coriolis Force). Water currents come from the west coast of Africa across to northeastern South America and then up and across the Caribbean to the southern tip of Florida where they form the Gulf Stream. One of the best documented cases of flotsam dispersal involves a West Indian vertebrate, green iguanas (*Iguana iguana* Linnaeus), and is consistent with this pattern. The distribution of this species and hurricane paths suggest that the iguanas originated in Guadeloupe and were transported to Anguilla, about 250 km to the northwest (Censky et al., 1998).

The closest relatives of most West Indian terrestrial vertebrates (excluding birds, bats, and freshwater fishes) are in South America, a fact that is compatible with the hypothesis that current flow is responsible for most overwater dispersal. The Amazon and many other major rivers in northeastern South America (Guiana Shield) drain into the Guiana Current, which flows into the Caribbean, and presumably carried the ancestors of much of the West Indian biota (Fig. 4). The closest relatives of a few West Indian vertebrates (Hedges, 1996c) and plants (Guppy, 1917) are in Africa. In those cases, the dispersal event would have taken at least several months based on the present rate of current flow (Guppy, 1917).

The West Indies has been north of the equator since the origin of the Caribbean Plate, and therefore the general east-to-west current flow would have been the same in the past, even prior to the emergence of the Isthmus of Panama (Fig. 3). An argument has been made elsewhere (Iturralde-Vinent & MacPhee, 1999) that a dry land bridge between South America and the Greater Antilles in the mid-Cenozoic would have altered that general current flow. In addition, those authors have argued that, based on past ocean current flow, most animals carried on flotsam during that time would not have ended up on islands in the West Indies. However, these suggestions are speculative (see below). Even in the presence of such a land bridge, the North Atlantic Gyre still would have

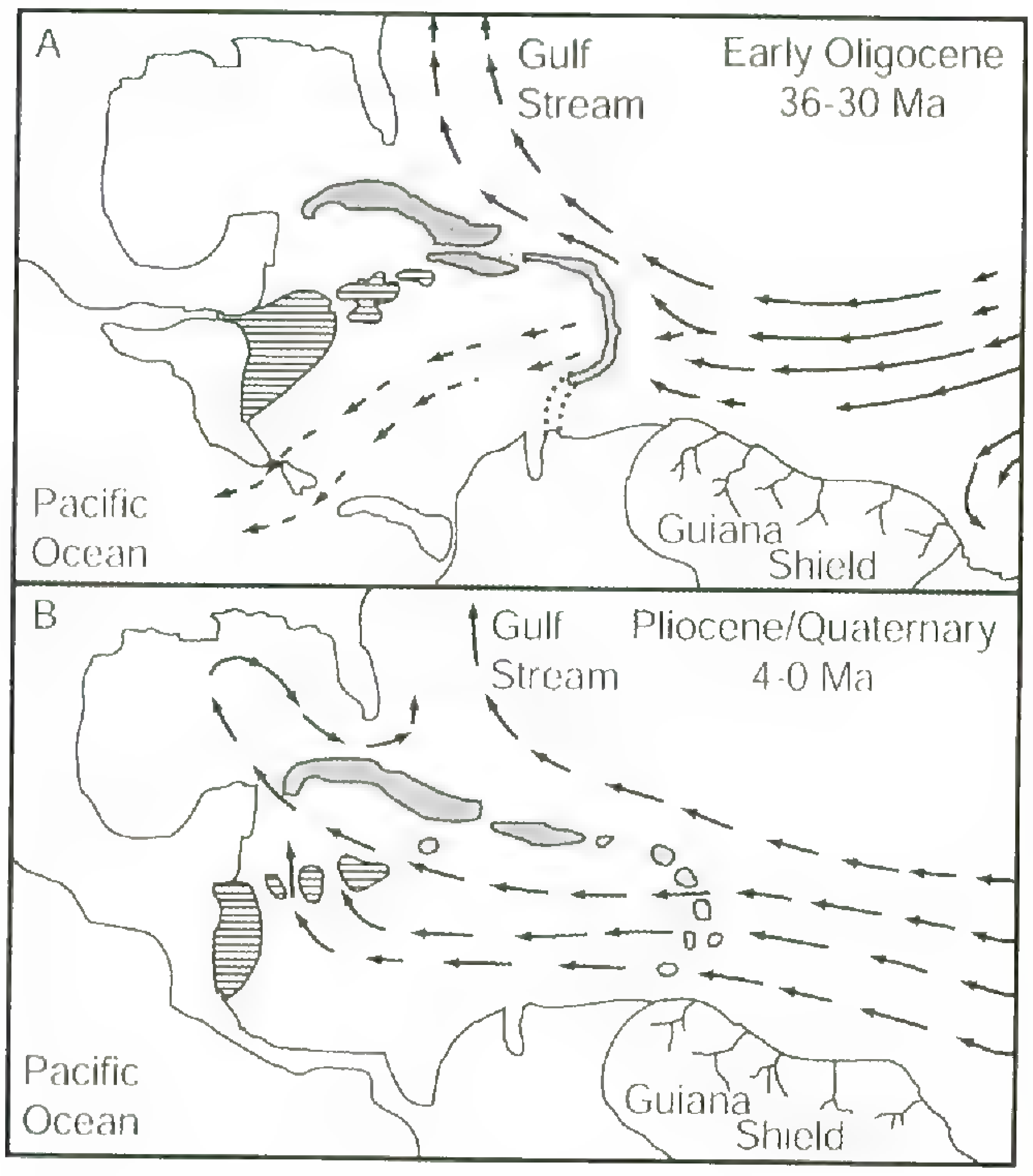

Figure 3. Water current patterns in the West Indies in the (A) Early Oligocene (36–30 Ma) and (B) Pliocene/Quaternary (4–0 Ma), after Hedges (Copyright 2001 from *Biogeography of the West Indies: Patterns and Perspectives* by C. A. Woods & F. E. Sergile (editors). Reproduced by permission of Routledge/Taylor & Francis, LLC.). Current flow along the Guiana Shield (Guiana Current) in the past is inferred given its paleolatitude at that time. Carbonate platforms (horizontal bars) may have affected current flow in the Caribbean (Droxler et al., 1998). —A. Early Oligocene. If the Aves Ridge (shaded crescent) was submerged or was a chain of islands (Droxler et al., 1998) some current flow (dashed arrows) would have passed on to the Pacific Ocean, as it did during the Miocene. If the Aves Ridge were a dry land bridge (dotted lines) the Guiana Current would have been deflected to the northwest along the Antillean landmasses and up to the Gulf Stream. Under both scenarios, rivers in northeastern South America draining into the prevailing current would have provided a source of flotsam for the Antilles. —B. Pliocene/Quaternary. The Guiana current continues to flow along the coast of South America and into the Caribbean, bringing flotsam to the Antilles.

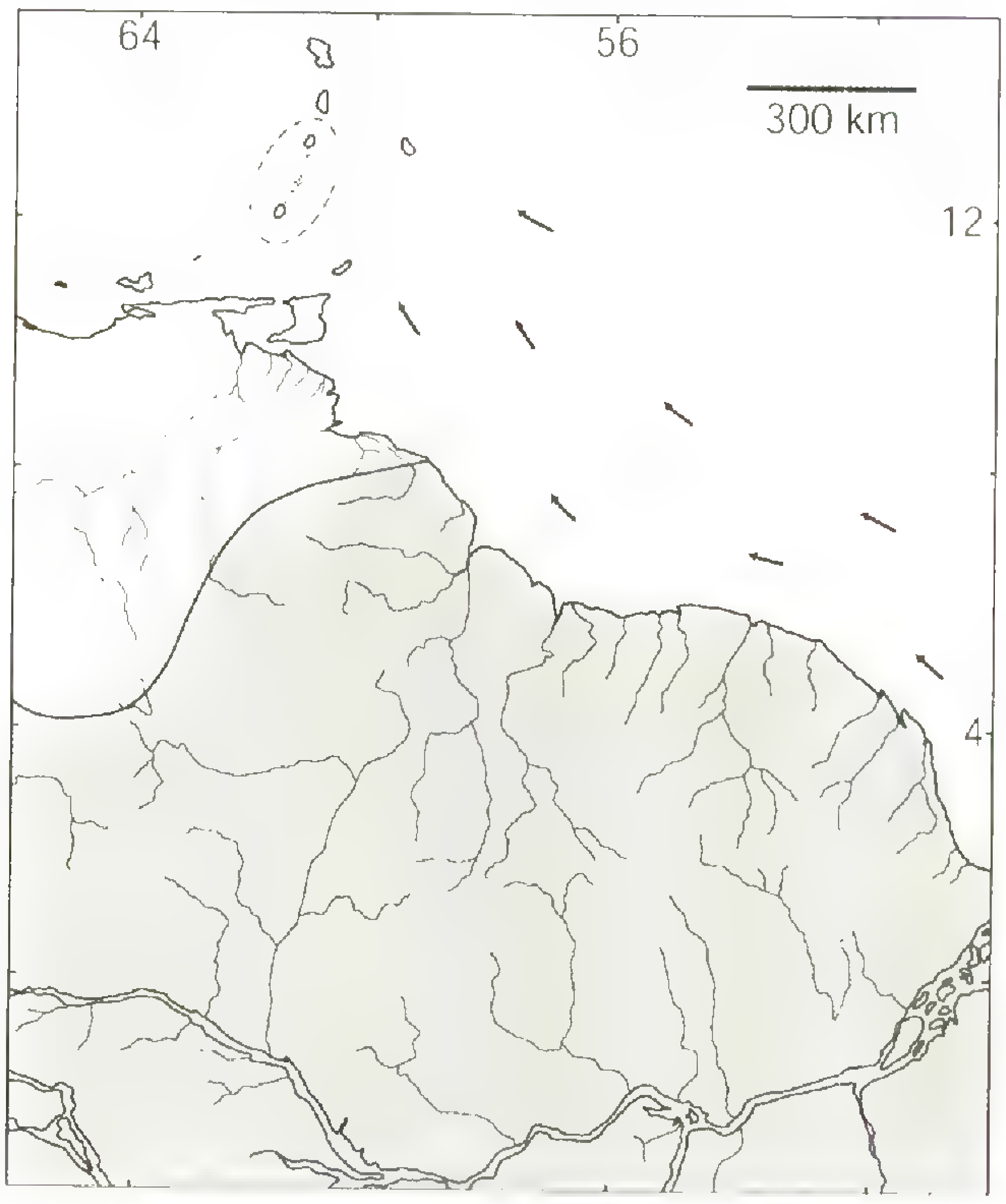

Figure 4. Distribution of a species of snake (*Corallus hortulanus* Linnaeus; shading) in South America and its closest relatives (*C. cooki* Gray and *C. grenadensis* Barbour; dashed lines) in Lesser Antilles (Henderson & Hedges, 1995; Henderson, 1997). Based on their distributions, and the direction of current flow, the island endemics likely arose by dispersal from South America of a snake (or snakes) floating on flotsam in the Guiana current (arrows).

brought currents from northeastern South America to the Antilles (Fig. 3; Hedges, 2001). Also, the focus on where flotsam from particular rivers in South America would go, rather than on where flotsam reaching the Greater Antilles originated, was an error in logic. If lizards riding on flotsam from a river in northwestern South America were carried out to the Pacific in the mid-Cenozoic (Iturralde-Vinent & MacPhee, 1999), that was their unfortunate luck. To understand the origin of the Antillean fauna, the hits are important; the misses do not count. If the Antillean hits are still mostly from South America, as opposed to Central and North America, those arguments concerning misses are of no consequence. Even if the implication is that fewer hits would occur, that also is of little consequence when the odds being discussed already are as low as one in 65 million years.

Hurricanes

Hurricanes are important for Caribbean biogeography because flotsam usually is the result of storm action (King, 1962) which affects air and water currents. For geographic and climatic reasons, the West Indies represents a hot spot for hurricanes, and most storm tracks are similar in direction to the surface current flow (Fig. 5). Thus, hurricanes and current flow work together to give a strong directionality for over-water dispersal in the West Indies. For example, it would be difficult for flotsam (or organisms) to travel from Cuba to the Lesser Antilles; the reverse would be much more likely. Although hurricanes may generate at least some flotsam in the West Indies (Censky et al., 1998), thunderstorms probably are responsible for nearly all flotsam emanating from rivers in South America.

Despite the directionality of dispersal mechanisms in the West Indies, some exceptions exist. For example, in 1999, the rare west-to-east Hurricane Lenny began near the Cayman Islands and ended near Nevis in the Lesser Antilles (Fig. 5). This unusual direction gave it the nickname "Lefty." Although west-to-east tracks are rare (only two others during the last five years), this indicates that some unusual distribution patterns might be explained by atypical hurricanes. Another possible factor is the counter-

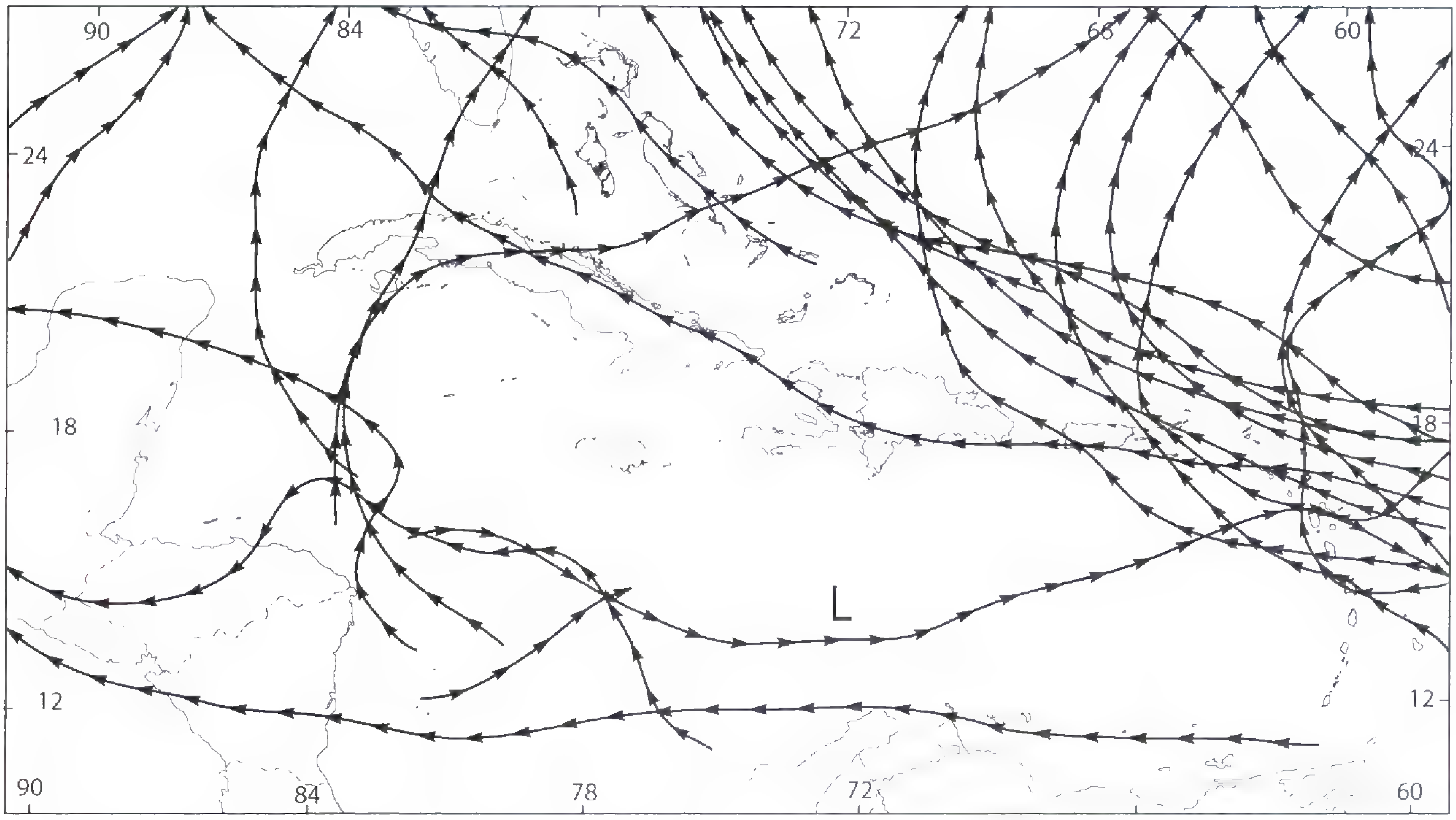

Figure 5. Hurricane tracks in the West Indies (1995–1999). The hurricane track labeled "L" is Lenny (also called "Lefty") of 1999. Source of hurricane track data: National Oceanic and Atmospheric Administration.

clockwise airflow of the hurricane vortex itself. Although the hurricane track may be moving in a westerly direction, strong surface winds to the south of the storm will be moving in the opposite (easterly) direction. This would not explain dispersal over long distances but might be a factor for short (tens of kilometers) distances, such as between islands (Powell, 1999).

Contemporary Models of Historical Zoogeography

In the several decades since plate tectonics became accepted, zoogeographers have had to consider the complexities introduced by past movements of islands. Early on, a new biogeographic theory was proposed suggesting that much of the West Indian biota originated on a proto-Antillean land area connecting North and South America in the late Cretaceous (Rosen, 1975, 1985). According to this vicariance model, the present-day Antillean fauna did not arrive by dispersal but instead was carried on the islands as they drifted, tectonically, to their current positions. Subsequent geologic models for the Caribbean differ considerably in details but not in the general notion of a proto-Antillean arc. However, as discussed above, the paleogeographic details concerning which land areas were emergent (and when), critical for this vicariance model, are still poorly known.

Advocates of the vicariance model have used phylogenetic relationships of organisms, almost exclusively, as evidence (Guyer & Savage, 1986; Crother & Guyer, 1996). This has been done with the assumption that the historical pattern of land area relationships should be reflected in the phylogeny of organisms that underwent vicariance (Rosen, 1975, 1985). A similar application of this approach was attempted for West Indian mammals (Dávalos, 2004). However, dispersal patterns often have directionality, as in the Caribbean, and can yield concordant phylogenies of groups (Hedges et al., 1994; Hedges, 1996b, c, d). Also, reconstruction of land area relationships in the West Indies is not yet possible because of uncertainty in details of the geologic history and paleogeography.

Other approaches to clarifying the vicariance vs. dispersal problem integrate multiple sources of information, including times of divergence of species and groups. The fossil record has been used in an indirect manner to show that times of divergence (i.e., the origin of West Indian groups) are too recent to support an origin by vicariance (Pregill, 1981). However, fossil-based divergence times are always minimum estimates. Time estimates from molecular data pertain to the actual splitting event because genetic differences begin to develop immediately following speciation. The most extensive molecular data available for testing these competing models of Caribbean biogeography have been immunological estimates of protein sequence divergence in serum albumin of West Indian vertebrates (Fig. 6). Generally, time estimates from these data have been too recent to support proto-Antillean vicariance (Hass,

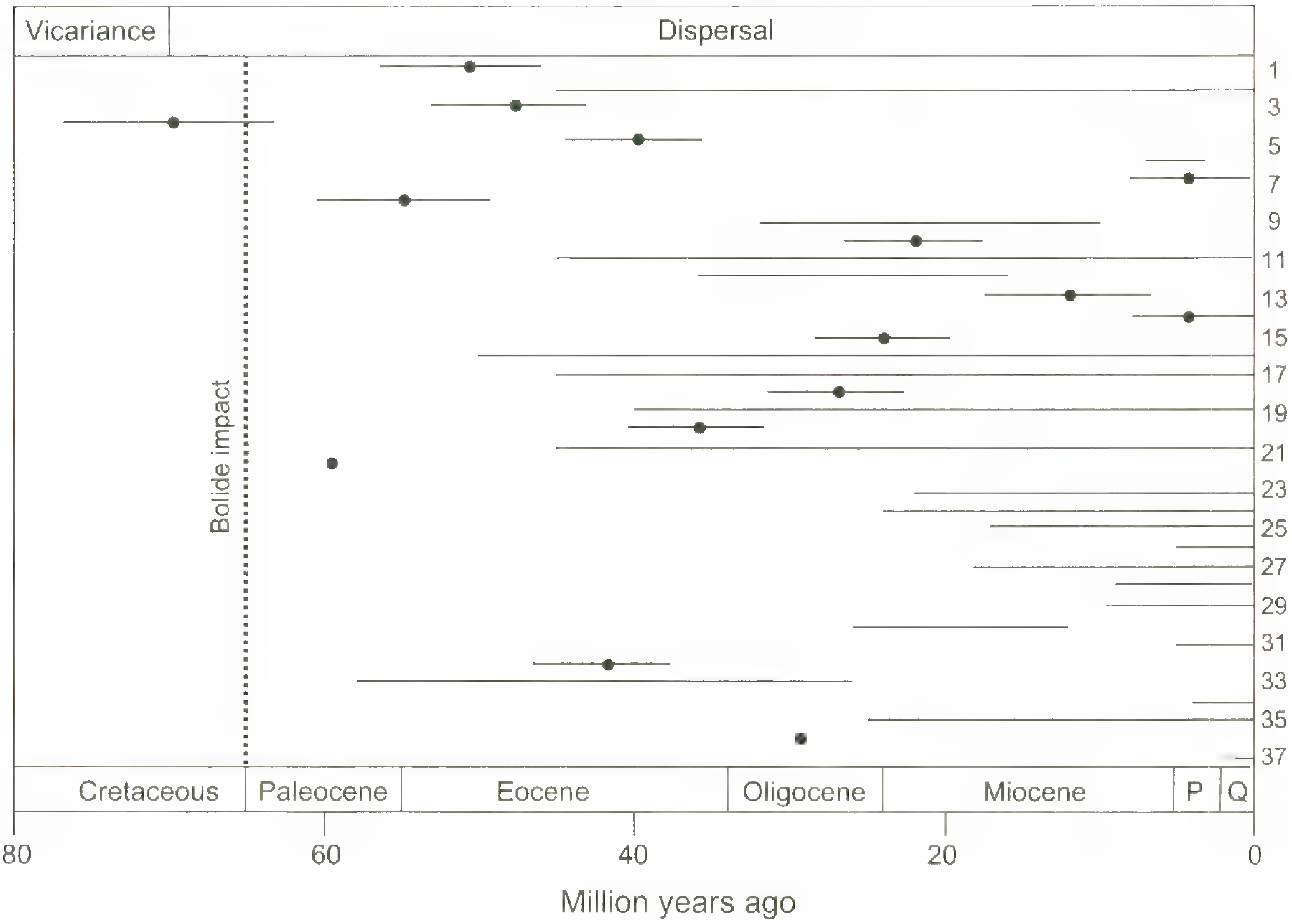

Figure 6. Times of origin for the 37 independent lineages of endemic West Indian amphibians and reptiles, mostly from immunological estimates of sequence divergence in the protein serum albumin (redrawn and modified with permission from Hedges, 1996c). Means and error estimates (in some cases, ranges) are shown. The lineages (indicated by numbers at right) are: (1) *Bufo peltocephalus* Tschudi group, (2) *Colostethus chalcopis* Kaiser, Coloma & Gray, (3) *Osteopilus* Fitzinger, (4) *Eleutherodactylus* Duméril & Bibron, (5) *Leptodactylus albilabris* (Gunther) Boulenger, (6) *Leptodactylus fallax* Müller, (7) *Crocodylus rhombifer* Cuvier, (8) *Amphisbaena* Linnaeus, (9) *Celestus* Gray, (10) *Diploglossus* Wiegmann, (11) *Gymnophthalmus pleei* Bocourt, (12) *Anolis* Daudin, (13) *Cyclura* Harlan, (14) *Iguana delicatissima* Laurenti, (15) *Leiocephalus* Gray, (16) *Aristelliger* Cope, (17) *Phyllodactylus pulcher* Gray, (18) *Sphaerodactylus* Wagler, (19) *Tarentola* Gray, (20) Antillean *Ameiva* Meyer, (21) *Cnemidophorus vanzoi* Baskin & Williams, (22) *Cricosaura typica* Gundlach & Peters, (23) *Epicrates* Wagler, (24) *Chironius vincenti* Boulenger, (25) *Mastigodryas bruesi* (Barbour) Schwartz & Henderson, (26) *Clelia errabunda* Underwood, (27) *Liophis cursor* Schwartz & Henderson group, (28) *Coniophanes andresensis* Schwartz & Henderson, (29) *Tretanorhinus variabilis* Duméril, Bibron & Duméril, (30) alsophine snakes, (31) *Leptotyphlops columbi* Klauber, (32) *Tropidophis* Bibron in de la Sagra, (33) *Typhlops* Oppel, (34) *Bothrops* Wagler, (35) *Trachemys* Agassiz, (36) pelomedusid turtles, and (37) *Geochelone* Fitzinger. Note: P = Pleistocene, Q = Quaternary.

1991; Hedges et al., 1992; Hass et al., 1993; Hedges et al., 1994; Hedges, 1996c; Hass et al., 2001). Also, those divergence time estimates are not strongly clustered at one particular point in time but tend to be more spread out, as one would expect from the action of a random mechanism such as over-water dispersal (Hedges, 1996c). One possible exception is the frog genus *Eleutherodactylus*, which may have arrived in the West Indies in the late Cretaceous or early Paleogene (Hass & Hedges, 1991; Hedges, 1996c). It is widespread, abundant, and diverse (i.e., not relictual), and the divergence times estimated between mainland and Antillean species are in the late Cretaceous or early Paleogene (Hass & Hedges, 1991; Hedges et al., 1992).

The phylogenetic relationships of West Indian vertebrates reveal that most have their closest relatives in South America (Hass, 1991; Hedges, 1996a, c). Among the exceptions are organisms that actively disperse, such as most freshwater fishes, bats, and birds. In those cases, geographic distance rather than current patterns appear to be more important since such organisms show closer affinities with Central and North American faunas.

The reduced higher-level taxonomic diversity remains a major piece of evidence in the comparison of contemporary models. The vicariance model predicts that the Antillean fauna should be a cross section of the continental fauna. Extinction is not excluded under the vicariance model, but no evidence exists in the fossil record that many major continental groups ever were present. For example, no primary freshwater fishes (intolerant of salt water), salamanders, caecilians, marsupials, carnivores, or lagomorphs are known to have occurred in the islands. Most families of frogs, turtles, and snakes are also

missing. Ungulates with their large bones fossilize well, yet no record of any ungulate exists aside from the early ca. 50 Ma rhinocerotoid from Jamaica, as noted above.

Other evidence that this peculiar taxonomic composition extended into the past comes from the unusually large radiations of some groups, such as ground sloths, capromyid rodents, eleutherodactyline frogs, and anoline and sphaerodactyline lizards. This is to be expected when niches are left vacant and is characteristic of oceanic islands never connected to continents (Williams, 1989; Woods, 1990; Hedges, 1996a). Probably as a result of these open niches, some of the largest and smallest species of various groups occur on islands, including the West Indies (Estrada & Hedges, 1996; Hedges & Thomas, 2001).

In addition to dispersal and vicariance, organisms may have reached the Greater Antilles by way of a land bridge (Rosen, 1975; Holcombe & Edgar, 1990; Woods, 1990; MacPhee & Iturralde-Vinent, 1994, 1995; Iturralde-Vinent & MacPhee, 1999). Unlike earlier land bridge models, proposed before plate tectonics, this land bridge is based on modern geology. It proposes that the Aves Ridge, now below sea level, formed a chain of islands or dry land connection between northern South America and the Greater Antilles in the mid-Cenozoic. However, the difference between a stable (unbroken) land bridge and a chain of islands is important for biogeography. Even narrow land bridge corridors, such as the current Isthmus of Panama, allow a major interchange of faunas (Stehli & Webb, 1985; Williams, 1989). A chain of islands, on the other hand, acts as a filter selecting for species with more optimal dispersal abilities. The Aves Ridge has been assumed to have been at least a chain of islands, much like the Lesser Antilles, that enhanced the over-water dispersal of organisms to the Greater Antilles (Rosen, 1975; Perfit & Williams, 1989). Thus, the recent assertion that the Aves Ridge was a dry and unbroken land bridge (Iturralde-Vinent & MacPhee, 1999) is of interest here. This model proposes only a narrow window of time (35–33 Ma) when this terrestrial corridor existed (Iturralde-Vinent & MacPhee, 1999).

In the process of providing evidence for their dry land bridge model, Iturralde-Vinent & MacPhee (1999) eliminated the possibility of proto-Antillean vicariance and gave arguments against over-water dispersal. They suggested that the Aves Ridge land bridge played a major role in the origin of West Indian terrestrial vertebrates. However, the same evidence that supports over-water dispersal for much of the West Indian fauna and argues against proto-Antillean vicariance also argues against the Aves Ridge land bridge model. This includes a reduced higher-level taxonomic diversity (now and in the past), unusually large adaptive radiations of groups present, and divergence time estimates that are not strongly clustered at one point in time. The existence of a land bridge would instead predict a more continental-like fauna (at least in the Paleogene fossil record) and divergence time estimates clustered strongly around 35–33 Ma. Nevertheless, because the Aves Ridge was probably a chain of islands, it should be expected to have enhanced dispersal at different times in the Cenozoic, e.g., mid-Cenozoic, much like the Lesser Antilles in the Late Cenozoic. In that respect it may have facilitated dispersal of mammals and other groups from South America to the Greater Antilles, as suggested by previous researchers (Holcombe & Edgar, 1990; Woods, 1990). However, this is different from the dry land connection claimed by Iturralde-Vinent & MacPhee (1999), which would have permitted a diverse cross section of the South American biota to enter the Antilles. Such a diverse cross section is not seen in the fauna.

The dry land bridge initially was proposed as a way to explain the origin of Antillean land mammals (MacPhee & Iturralde-Vinent, 1994, 1995). For example, Iturralde-Vinent & MacPhee (1999: 58) stated that they “doubt that the sloths swam the distance.” Yet, as they acknowledge, some species of ground sloths were highly adapted to marine life (Muizon & McDonald, 1995), thus removing this proposed biological need for a dry land bridge. Unfortunately, the creation of a dry land bridge also has implications for other aspects of the paleogeography of Iturralde-Vinent & MacPhee (1999); as previously mentioned it is used to suggest the direction of water current flow in the past and its influence on dispersal.

Iturralde-Vinent & MacPhee (1999) also claim that no permanent landmasses were present in the Caribbean prior to the middle Eocene, eliminating the possibility of proto-Antillean vicariance. Although the absence of direct evidence for an uninterrupted land occurrence is used as support of that claim, there is also an absence of direct evidence *against* uninterrupted land occurrence. In fact, such evidence would be difficult to obtain, as it would require nearly continuous sedimentation present from all areas and sampled at all time intervals. Because some land areas were at least close to the ocean surface (sea level) during part of that time, as acknowledged by Iturralde-Vinent & MacPhee (1999), the possibility of uninterrupted land areas cannot be completely ruled out. Moreover, organisms are surprisingly resilient to changing landscapes and are known to survive as continuous lineages for millions of years in island chains such as the Hawaiian Islands and Galapagos

Islands (Sequeira et al., 2000). In these cases, temporal continuity in the long term is likely accomplished by dispersal among ephemeral islands in the short term. Thus, the biota of an archipelago can be maintained over time even while individual islands rise and fall.

The Problem of Relictual Groups

Two endemic groups of West Indian animals, the giant shrews (*Solenodon* Brandt) and Cuban night lizards (*Cricosaura* Gundlach and Peters), have been suggested to have arisen through proto-Antillean vicariance (MacFadden, 1980; Hedges et al., 1991; Hedges et al., 1992; Roca et al., 2004). However, the distributions of both groups, including mainland relatives, have receded through time (i.e., are relictual), which presents a problem for interpreting their biogeographic history. Before discussing these biogeographic implications, some clarification is needed concerning the estimated time of divergence for the Cuban night lizards from their closest relatives in the family Xantusiidae.

The lizard family Xantusiidae occurs in North and Central America and the West Indies. Only one species is known from the West Indies, *Cricosaura typica* Gundlach and Peters, restricted to a small region of eastern Cuba. In the original studies reporting the xantusiid lizard sequence data (Hedges et al., 1991; Hedges & Bezy, 1993), the authors suggested that *Cricosaura* might represent a remnant of the proto-Antillean fauna, based on molecular phylogeny and fossil data. Although a molecular clock analysis was not explicitly used, they demonstrated phylogenetically that the West Indian lineage (*Cricosaura*) was the most ancient in the family, and its divergence from other xantusiids must have logically predated fossils of *Palaeoxantusia fera* Hecht (ca. 60 Ma) assigned to the other lineage (Savage, 1963; Schatzinger, 1980; Hedges et al., 1991).

Those sequence data were reanalyzed later by Vicario et al. (2003), who recovered the same topology and performed a molecular clock analysis, arriving at a different conclusion concerning the time of origin of the *Cricosaura* lineage. Although much emphasis was given to this difference, it was the sole result of those authors removing the ca. 60 Ma fossils of *Palaeoxantusia fera* from consideration, without explaining why they disagreed with earlier authorities concerning that fossil. Using the next earliest fossils (ca. 43 Ma) for calibration of a mainland divergence (*Xantusia* Baird/*Lepidophyma* Duméril), their molecular clock time interval for the *Cricosaura* divergence from other xantusiids was 64.9–43 Ma. They stated that this estimate "is not consistent with the Hedges et al. (1992) proposal that the *Cricosaura* line survived the bolide impact at the K/T (Cretaceous/Paleogene) boundary at 65 MYBP, as the earliest limit of our estimate is nearly 100,000 years after that momentous event" (Vicario et al., 2003: 257). However, there are several problems with this interpretation: (1) they ascribed considerably more accuracy to molecular clocks than is justified (e.g., the difference between 64.9 and 65.0 Ma is only 0.15%), especially given the modest sequence data set, (2) they conceded that the calibration could be off by 17 million years, which nullifies the difference of 100,000 years, and (3) they interpreted the divergence date as a fixed time estimate, when it is more correctly interpreted as a minimum (Hedges & Kumar, 2004).

The same data were reanalyzed more recently by Roca et al. (2004), who disagreed with Vicario et al. (2003) and supported the earlier (Cretaceous) divergence for *Cricosaura*, at 76 Ma. They used a different method of time estimation (Thorne et al., 1998) with the same calibration point (43 Ma for *Xantusia*/*Lepidophyma*) as minimum and added *Palaeoxantusia fera* (60 Ma) as maximum. To explore the effect of calibration point on this time estimate, I reanalyzed the data using the same methods but used instead *Cricosaura*/non-Caribbean divergence for calibration (a Bayesian estimate can be obtained even for calibrated nodes). Regardless of whether that node is treated as a fixed calibration or minimum calibration, at 43 Ma or 60 Ma, and regardless of the ingroup root prior (50–100 Ma), the confidence interval in all cases extends into the Cretaceous. If *Palaeoxantusia fera* is correctly assigned to the *Xantusia*/*Lepidophyma* lineage, then a fixed calibration of 60 Ma for the *Cricosaura*/non-Caribbean split is the preferred method, yielding a time of 75 Ma (60–116 Ma) using an ingroup prior of 75 Ma, similar to the result of Roca et al. (2004). This date should then be interpreted as a minimum time estimate and not a mean time estimate in drawing conclusions.

The time of divergence of the West Indian shrews (*Solenodon*) from their closest relatives on the mainland was estimated to be 76 Ma (72–81 Ma) using a large sequence data set of 16 nuclear and three mitochondrial genes (Roca et al., 2004). A direct interpretation of this ancient divergence for the shrews and for xantusiid lizards is that the West Indian representatives originated by vicariance on the proto-Antilles in the late Cretaceous, whether it was dry land or an island chain, and survived the bolide impact in that region at 65 Ma. However, both of these groups appear to be relictual, which means that alternative hypotheses should be considered. Xantusiid lizards are patchy in distribution and have clearly receded from a wider distribution in the past (Hedges

et al., 1991; Sinclair et al., 2004). As noted by Roca et al. (2004), there is uncertainty regarding the identification of the closest relatives of West Indian shrews. Nonetheless, some North American soricomorphs (e.g., *Apternodus* Matthew), all extinct, have been proposed, and the general conclusion is that solenodontoids and their relatives represent a relictual group of animals (MacFadden, 1980).

The primary alternative hypothesis raised by these relictual groups, such as West Indian shrews and xantusiid lizards, is that they arose by dispersal from the mainland in the early Paleogene and not by vicariance in the late Cretaceous (Hedges, 1996a). According to this hypothesis, the phylogenetic divergence still occurred in the Cretaceous, as estimated by molecular clocks, but it resulted in descendant lineages that initially occupied only mainland areas. At some later time, in the Paleogene, dispersal occurred from the mainland to the West Indies, with the mainland representatives of those "West Indian" lineages later becoming extinct. Advantages of this hypothesis are that it does not require the presence of emergent land in the Antilles since the Cretaceous and survival of the local effects of the bolide impact (65 Ma) by the Antillean group. Nonetheless, a better fossil record of mainland relatives would help to distinguish between this hypothesis and one of vicariance. Currently, neither hypothesis can be strongly favored.

Dispersal from Islands to Mainland

In discussions of island biogeography, dispersal is usually considered to be in one direction: from the mainland to the island or islands (Cox & Moore, 2005). However, the Greater Antilles are large and old land masses capable of being source areas for dispersal. At least three Antillean groups appear to have colonized mainland areas. At some time during the mid-Paleogene, estimated as 37 Ma with a molecular clock, one or more frogs (*Eleutherodactylus*) dispersed from Cuba to the adjacent mainland of Central America (Hedges, 1989; Hass & Hedges, 1991; Hedges et al., 1992). The founders evolved into a clade of *Eleutherodactylus* species recognized today as the subgenus *Syrrhophus* Cope (Hedges, 1989). Some Central American pond turtles of the genus *Trachemys* Agassiz (Seidel, 1988, 1996) and a large clade of anoline lizards (Nicholson et al., 2005) are also considered to have originated by dispersal from the Antilles to the mainland. The West Indies was probably the source for other mainland groups as well, and this should be considered in any discussions of Caribbean biogeography.

Conclusions

This brief overview of West Indian biogeography focuses on the major competing models. Anyone familiar with the literature will admit that this field generates contrasting opinions. In part, this is because of the complexity of the problem and evidence that is often limited. All agree that over-water dispersal can and has occurred, but some dispute the degree of the contribution of this mechanism. The paleogeographic basis for the other two proposed mechanisms, proto-Antillean vicariance and a mid-Cenozoic land bridge, has not yet been confirmed. In the author's opinion, both of those mechanisms remain as possibilities, however remote, and the author disagrees with the assertion that proto-Antillean vicariance must be ruled out (Iturralde-Vinent & MacPhee, 1999). At the same time, paleogeographic evidence does not currently support the Aves Ridge land bridge model, in contrast to claims by its strongest advocates Iturralde-Vinent and MacPhee (1999). In their advocacy of that model, with the corresponding need to construct a mid-Cenozoic walkway for land mammals, they have blurred the distinction between paleogeography (past landscapes) and historical biogeography (past distributions of organisms). They refer to their model as "paleogeography" but in reality it is a biogeographic model biased by their desire to create a corridor for mammals when there is no physical evidence to support such an unbroken corridor of land. Biologists and biogeographers need unbiased paleogeographic reconstructions to evaluate their evidence from organisms.

As noted here, and in more detail elsewhere (Hedges, 1996a, c, 2001), the weight of the evidence supports an origin by over-water dispersal for most of the West Indian vertebrate fauna. This conclusion stems from (1) the reduced higher-level taxonomic composition of the fauna (now and in the past), (2) the presence of unusually large adaptive radiations, (3) the finding that closest relatives of most Antillean groups are from South America (passive dispersers) or Central and North America (active dispersers), and (4) the finding of divergence time estimates that are not strongly clustered. The first point was noted over a century ago and has been dubbed more recently as the central problem (Williams, 1989). The second point is related to the first, and infers that existing groups have taken over niches of the missing groups (thus suggesting that the missing groups have been missing for a long time and not just recently extinct). The third point is consistent with the directionality of water current flowing through the region (now and in the past). The fourth point follows the prediction of over-water dispersal.

Despite this general (major) pattern, several Antillean groups may have originated on the proto-

Antilles in the Late Cretaceous or dispersed there in the early Paleogene. These include the Cuban gars (fish), eleutherodactyline frogs, the xantusiid lizard *Cricosaura*, and the insectivore mammals. Additional data are needed for these and other so-called ancient groups. In the future, divergence time estimates will be based on sequence data from multiple genes, rather than immunological estimates from a single protein, and therefore will increase in precision. Such time estimates from many Antillean groups will permit a more accurate test of these competing models.

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THE GREAT AMERICAN BIOTIC INTERCHANGE: PATTERNS AND PROCESSES[1]

S. David Webb[2]

Abstract

When the Panamanian land bridge was emplaced about 2.7 Ma, it triggered the Great American Biotic Interchange (GABI), a major mingling of land mammal faunas between North and South America. Four families of northern immigrants (Procyonidae, Felidae, Tayassuidae, and Camelidae) diversified at moderate rates, while four others, Canidae, Mustelidae, Cervidae, and especially Muridae, evolved explosively. As a consequence, half of living South American genera are descendants of northern immigrants. The other major consequence of the interchange was the conquest of tropical North America by immigrants from Amazonia, an episode that justifies the term Neotropical Realm.

Key words: biostratigraphy, evolutionary rates, isthmian land bridge, mammals, Neotropical Realm.

Resumen

Cuando el corredor terrestre panameño se ubicó hace cerca de 2.7 Ma, desencadenó el Gran Intercambio Biótico Americano (GABI), una mezcla importante de las faunas de mamíferos terrestres entre América del Norte y del Sur. Cuatro familias de inmigrantes del norte (Procyonidae, Felidae, Tayassuidae, and Camelidae) se diversificaron a un ritmo moderado, mientras que otras cuatro, Canidae, Mustelidae, Cervidae y especialmente Muridae, evolucionaron en forma explosiva. Por consiguiente, la mitad de géneros suramericanos actuales son descendientes de inmigrantes del norte. La otra principal consecuencia del intercambio fue la conquista de Norteamérica tropical por inmigrantes amazónicos, un episodio que justifica el término de Reino Neotropical.

The roots of the Latin American biota can be traced down through the epochs of earth history to several formative chapters. During most of the Mesozoic Era, the South American biota was an integral part of the Gondwanan biota. Through most of the Cenozoic Era, the terrestrial and freshwater biotas of South America were isolated from those of North America and all other continents by deep ocean troughs. The most recent chapter begins with the Great American Biotic Interchange (GABI). This occurred approximately three million years ago during the late Pliocene, when the powerful forces of plate tectonics raised the isthmian land bridge in a final phase of uplifting the northern and southern cordilleras to connect them as the backbone of the Americas. Such dramatic physical changes inevitably triggered major new biological interactions between the two previously separate American continental biotas, and that is the focus of this paper.

In the following pages, I consider the major evolutionary features of the GABI as registered by land mammals. The mammals offer the richest, most nearly coherent record of faunal changes in both American continents during the late Cenozoic. The living faunas, along with their fossil predecessors, record both the rapidly changing distributions and the dynamic evolutionary diversifications that illuminate the origins of the Latin American biota.

My own introduction to the nature of the GABI began in the 1960s when the Florida Museum of Natural History was actively filling chronological gaps in that state's rich late Cenozoic record of land vertebrates. One fossil site in particular opened a critical window into the late Pliocene, which is known in the system of North American land mammal ages as the Blancan. Unlike any preceding stage, that interval introduced to North America a large cohort of land mammals previously restricted to South America.

Our site, Inglis 1A (Fig. 1), yielded the richest sample of late Pliocene vertebrates in eastern North America. Our team excavated and screenwashed about 100 tons of fossiliferous sediment, which yielded about 120 species of land and freshwater animals. Early in our studies, I realized that ten genera of new immigrant taxa from South America accounted for about 20% of the entire rich fauna (Webb, 1976). There were three families of ground sloths; three families of shelled edentates, ranging

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Figure 1. Paleontological excavations by the Florida Museum of Natural History at Inglis 1A (late Pliocene) at cross-state barge canal, west-central Florida. Photo by author.

from tiny *Dasypus* to gigantic †*Glyptotherium*[3]; as well as two families of rodents, namely Erethizontidae and Hydrochoeridae. The truly surprising forms were a vampire bat, *Desmodus* Wied, and a giant predaceous bird named †*Titanis* Brodkorb. Additionally, nearly 40% of the fauna at Inglis 1A represented North American genera, representatives of which had dispersed to South America during roughly the same time in the late Pliocene. There were relatives of such living Neotropical taxa as llamas, peccaries, tapirs, jaguars, raccoons, foxes, and spectacled bears (cf. Table 1 for taxa). Thus, a majority of the land mammal fauna recovered from Inglis 1A, and living in Florida nearly three million years ago, were participants, in one direction or the other, of the GABI. I was also astonished to realize how similar the mingled elements of the Inglis 1A local fauna were to contemporaneous interchange faunas through the American tropics and all the way into Argentina and the "southern cone" of the continent. Thus, in Florida we had stumbled fortuitously into the acme of the GABI (Webb, 1976).

The interamerican evolution of land mammals represents a dramatic experiment in rapid cladogenesis on an intercontinental scale. We may ask how the modern South American fauna differ from the preceding fauna living in isolation. Likewise, we may ask how the present Central American fauna differ from the preceding fauna that had lived in the southern portion of North America. Clearly, the land bridge catalyzed a rapid remodeling of the Latin American fauna. Such geological changes represented the underlying cause that triggered major biological effects.

We begin by indicating some preliminary land mammal dispersals that preceded the GABI. I refer to these as herald taxa. Thereafter, we will consider the much larger cohorts that burst across a fully accessible Panamanian land bridge, which I refer to as legions taxa. We also briefly review current geochronological evidence regarding the timing of the GABI. Finally, we will consider evolutionary and ecological factors that influenced the origin of the South and Central American land mammal faunas.

Herald Taxa

A very small number of interamerican land mammal dispersals have been recorded earlier than the latest Pliocene in North and South America. These

[3] † represents extinct taxa.

Table 1. Families of land mammals in the GABI.

Family	Common name
Northern legion taxa (17 families)	
Soricidae	shrews
Leporidae	rabbits
Heteromyidae	pocket mice
Geomyidae	pocket gophers
Sciuridae	squirrels
Muridae	field mice
Felidae	cats
Mustelidae	skunks and otters
Canidae	foxes and wolves
Procyonidae	raccoons
Ursidae	bears
Gomphotheriidae	elephantoids
Tapiridae	tapirs
Equidae	horses
Tayassuidae	peccaries
Camelidae	llamas
Cervidae	deer
Southern legion taxa (21 families)	
Didelphidae	opossums
Dasypodidae	armadillos
Chlamytheriidae	giant armadillos
Glyptodontidae	tank-like edentates
Megalonychidae	bear-sized ground sloths
Mylodontidae	middle-sized ground sloths
Megatheriidae	elephantine ground sloths
Bradypodidae	three-toed tree sloths
Myrmecophagidae	anteaters
Desmodontidae	vampire bats
Callithricidae	marmosets
Cebidae	New World monkeys
Hydrochoeridae	capybaras
Erethizontidae	porcupines
Caviidae	guinea pigs
Agoutidae	pacas
Dasyproctidae	agoutis
Echimyidae	spiny rats
Toxodontidae	rhinoceros-like ungulates
Trichechidae	sea cows
Phororhachidae	giant predaceous birds

herald taxa appear during the middle Miocene some six or seven million years earlier than the legion taxa. Both Mexico and Central America have increasingly strong records of late Cenozoic land mammals, yet in those areas no South American immigrants other than the herald taxa have been recognized before the latest Pliocene (Webb, 1997; Ferrusquia-Villfranca, 2003). Some native North American groups (e.g., the slingshot-horned Protoceratidae) that had become increasingly rare at temperate latitudes evidently thrived in the more tropical landscapes of Mesoamerica (Webb et al., 2003). As stated by Ferrusquia-Villfranca (2003: 321), all known mammal faunas in the Miocene of Mesoamerica "show strict North American affinities."

According to present records, the herald taxa consist of only two distinct genera of ground sloths in North America and one genus of large raccoon in South America. As indicated by Tedford et al. (2004), †*Thinobadistes* Hay, a mylodontid sloth, and †*Pliometanastes* Hirshfeld & Webb, a megalonychid sloth, arrived in the early Hemphilllian about 9 million years ago (Ma). One record of †*Pliometanastes* from California yields the best age estimate for these early immigrant sloth genera. There it occurs in sediments 4 meters below the Mehrten Tuff, which is radiometrically dated at 8.2 Ma (Hirschfeld & Webb, 1968).

†*Arctonasua* Baskin is a large procyonid, well known in North America during the Clarendonian and Hemphillian (Baskin, 2003). †*Cyonasua* Ameghino, a closely related genus, appears in the Chiquimil fauna of northwestern Argentina in the Huayquerian land mammal age, middle to late Miocene (Marshall, 1985; Flynn & Swisher, 1995). By Chapadmalalan time, †*Cyonasua* had been replaced by its very large descendant, †*Chapalmalania* Ameghino.

Flynn et al. (2005) suggested that two additional genera of South American ground sloths separately invaded North America. This suggestion is based on late Hemphillian collections from near Guanajuato in central Mexico. It may be more parsimonious, however, to view the two genera, identified as †*Megalonyx* Leidy and †*Glossotherium* Harlan, as North American descendants of the closely related sloth taxa already present in the early Hemphillian. The question may be resolved by more detailed analysis of the Hemphillian sloth material from Guanajuato.

For three reasons, the appearances of these herald taxa have been interpreted as waif dispersals, not as crossings of a continuous land bridge. Firstly, the hiatus of some six million years, during which no other crossings have been documented, suggests a fortuitous mode of island hopping. Secondly, living sloths and raccoons are particularly adept at floating and swimming, so that they are among the most likely groups of land mammals to make water crossings (Webb, 1985). Thirdly, the very limited number of other concurrent arrivals in either direction provides strong negative evidence that no broad highway had opened between 9 and 3 Ma. The strength of this interpretation depends on one's optimism about the completeness of relevant parts of the fossil record. Suffice it to state that the late Cenozoic record of land mammals in North and South America is exceedingly rich and continues to improve each year.

Occasionally, one reads that the murid rodents also jumped the isthmian gap and entered South America

before the latest Pliocene. One early paper by Marshall (1979) encouraged the idea of some mid-Tertiary murid immigration, even though the word "model" in the title made it quite clear that his discussion was hypothetical. In their discussion of the timing of the GABI at about 2.7 Ma, Woodburne and Swisher (1995) reiterate the possibility that two murid genera had reached South America during the Montehermosan stage, generally correlated with the latest Miocene and earliest Pliocene (ca. 7 to 4 Ma). The supposed records that they cite (by Reig, cited in Marshall, 1985), however, were not explicit and have not been verified by subsequent faunal and stratigraphic studies. Indeed, in his review of fossil murid records in the Pampean region of Argentina, Pardinas (1995: 229) finds the stratigraphic provenance of Reig's two type specimens to be "dubious."

An additional strong inference comes from paleontological studies of murids in Miocene-Pliocene sites in North America. There the presence of appropriate plesiomorphic sister groups such as †*Prosigmodon* Jacobs & Lindsay and †*Bensonomys* Gazin, just prior to the time of the interchange, strengthens the view that these lineages did not jump the gap prematurely. Jacobs and Lindsay (1984), for example, make a strong case for Miocene-Pliocene diversification of murids in North America followed by dispersal of multiple branches during, but not before, the Blancan GABI.

Legions Taxa

Table 1 records the families of land mammals that moved in each direction across the land bridge. In addition to including land and freshwater mammals, I have included the †Phororhachidae, a family of large, predaceous birds that followed some of their favorite mammalian prey northward across the land bridge. The record is based on †*Titanis* from Inglis 1A and other Blancan sites in Florida. These data indicate a balanced reciprocal faunal interchange, as noted by Webb (1976), Webb and Marshall (1982), and Marshall et al. (1982b). The body of paleontological evidence also indicates that the mingled fauna on each American continent supported a greater diversity than before the GABI. This increase in apparent diversity lasted about a half a million years before it decreased to its prior level (Webb, 1976; Marshall et al., 1982b). Wilson (1992: 120) explains this biogeographic pattern as follows: "When biologists see a number go up following a disturbance and then fall back to the original level, whether body temperature, density of bacteria in a flask, or biological diversity on a continent, they suspect an equilibrium." The interchange numbers neatly fit a large-scale example of the species equilibrium hypothesis. After the initial mutual enrichment of both continental faunas, they encounter limits to diversity, a kind of carrying capacity that limits the number of broadly similar mammalian groups that one continent can support.

Chronology of the Interchange

The reciprocal arrival of a cohort of terrestrial mammal immigrants deep within each of the two American continents marks the inception of the interamerican land bridge and a major faunal interchange. It is important to date the GABI as precisely as possible, because it represents the datum by which ensuing evolutionary and biogeographic changes can be calibrated.

The best method to date emplacement of the Panamanian land bridge comes, perhaps surprisingly, not from any geologic data in Panama but from excellent stratigraphic sequences with rich fossil faunas in temperate latitudes of North and South America. Only a few examples of this paleontological record need be cited here to establish the quality of the record and the basic chronological framework.

The Anza–Borrego Desert lies in southern California, just north of the Salton Sea Basin and within the San Andreas Fault zone. Sediments in that region accumulated very rapidly during the Pliocene and Pleistocene, first entombing marine fossils within the Imperial Formation, an arm of the Gulf of California, and later, non-marine vertebrates and their trackways within the Vallecito Creek Formation. The latter formation provides a wealth of land mammals, including early appearances of some South American immigrants, notably †*Erethizon stirtoni* (White) Frazier, in a vertical sequence of some 4000 meters. Furthermore, these fossil beds include a radiometric date of 2.3 Ma and are directly intercalated with a long, detailed paleomagnetic profile (Opdyke et al., 1977). Figure 2 exemplifies the outstanding exposures of long fossiliferous sections in the Anza–Borrego Desert.

An equivalent fossiliferous section in North America, in Arizona, known as the 111 Ranch Sequence, produces the Tusker Fauna, which is associated both with an ash dated at 2.33 Ma and an excellent magnetic profile (Galusha et al., 1984). Similarly, in southwestern New Mexico, local faunas from the lowermost strata in the Mesilla Basin (Mesilla A in the Camp Rice Formation) and Pearson Mesa clearly tie South American immigrants into magnetostratigraphically controlled sections (Morgan & Lucas, 2003).

In each of these southwestern examples, the new immigrants occur within an interval of normally oriented magnetic samples, constrained above by the

Figure 2. Vallecito Creek Formation Pliocene-Pleistocene exposures in Anza Borrego State Park, California. Dr. John A. White indicating collecting areas of Los Angeles County Museum. Photo by author.

radiometric date and the Gauss/Matuyama magnetic reversal boundary (fixed at 2.58 Ma) and below by the Kaena Subchron (at 3.04 Ma). On this basis, mammalian stratigraphers often cite the time of first appearance for Neotropical immigrants into North America as 2.6 or 2.7 Ma (Woodburne & Swisher, 1995; Bell et al., 2004).

The foregoing faunas from the southwestern United States that most concisely date the first appearances fall within the late Blancan land mammal stage. This same biostratigraphic rubric includes several Florida faunas, most notably the Inglis IA site, which records the greatest wealth of Neotropical immigrants from any one locality. The unfortunate absence of radiometric control on Florida faunas weakens our ability to specify how concurrently the entire cohort of Blancan immigrants from South America arrived in temperate North America. It is reasonable to suggest that they had all come within about a two-million-year period, for that is the approximate span of the Blancan interval (Bell et al., 2004).

Some evidence of Blancan immigrants comes from lower latitudes in Mesoamerica. One unique genus is †*Meizonyx* Webb & Perrigo from El Salvador. This megalonychid ground sloth is larger than any Blancan species within its temperate sister genus, †*Megalonyx*, yet it possesses triangular (plesiomorphic) caniniform teeth (Webb & Perrigo, 1985).

Intensive geochronological and biostratigraphic studies of sedimentary sequences near Guanajuato in central Mexico record several immigrant genera from South America earlier in the Blancan than the well-dated southwestern faunas cited above (Miller & Carranza-Castaneda, 2001; Flynn et al., 2005; Montellano-Ballesteros & Jimenez-Hidalgo, 2006). †*Plaina*, a small sister genus of †*Holmesina* Simpson, is recorded at about 4.6 or 4.7 Ma, in the very early Blancan. †*Glyptotherium* and †*Neochoerus* appear in the interval between 3.9 and 3.1 Ma (Flynn et al., 2005). This may suggest, as proposed by Flynn et al. (2005), that central Mexico represented a different mammalian province than southwestern United States. It is possible that some Florida Blancan faunas, notably Haile 15A and Santa Fe River 1, producing these and other immigrant land mammals from South America, may also pertain to the early Blancan. These faunas are not well enough constrained by geochronology, and it is notoriously difficult to distinguish early from late Blancan biostratigraphically (Bell et al., 2004). The new discoveries of earlier

Figure 3. Barranca de Los Lobos, Buenos Aires Province, Argentina, Pliocene-Pleistocene exposures. Photo by author.

Blancan immigrants in Guanajuato indicate that the legion taxa may have reached temperate North America on a more haphazard schedule than previously suggested.

Critical evidence from southern, temperate parts of South America produces results broadly similar to those from the southwestern United States. Long sequences of fairly continuous fossiliferous sediments provide an essential framework for integrating biostratigraphic evidence with both radiometric dates and paleomagnetic reversal chronology (Marshall et al., 1982a; Flynn & Swisher, 1995).

A central part of Barranca de Los Lobos near Mar del Plata in Argentina (Fig. 3), along with other typical Uquian sites in the province of Buenos Aires, records a number of first appearances of North American taxa, including equids, mustelids, tayassuids, camelids, and murid rodents (Pascual et al., 1985; Alberdi et al., 1995). Paleomagnetic work, integrated with land-mammal biostratigraphy, places these northern immigrants just below the Gauss/Matuyama boundary, justifying a first appearance datum of about 2.5 Ma (Marshall et al., 1982a), later revised to about 2.7 Ma (Woodburne & Swisher, 1995).

A curious claim of a much earlier immigration of northern land mammals into South America has been advanced by Campbell et al., (2000: 33A) in a brief abstract. Based on presumed correlations to sediments underlying an ash date of 9.01 Ma in the Madre de Dios Formation in eastern Peru, these authors recognize "numerous Amazonian paleofaunas" that include "at least two species each of proboscideans, peccaries, tapirs and camelids." The discrepancy between their evidence from unspecified Amazonian faunas versus the wealth of previously documented, late Miocene land mammal faunas in South America is profound. The classical sequences at Chiquimil and Corral Quemado in Catamarca Province, northwestern Argentina, offer a wealth of excellent fossil mammals typifying the Huayquerian land mammal stage. Additionally, rich faunas from Micana in the eastern altiplano of Bolivia also span relevant, late Miocene intervals (see recent references in Flynn & Swisher, 1995). Yet the only hint of any North American element in any of these well-studied faunas is †*Cyonasua*, discussed earlier from the Chiquimil fauna from Argentina (Marshall, 1985; Flynn & Swisher, 1995). Even the next younger Chapadmalalan and/or Montehermosan mammal ages give no hint of the mysterious immigration proposed by Campbell et al. (2000). In apparent anticipation of such skepticism, these authors claim that "ecological restrictions undoubtedly hindered the movement of the earliest dispersers out of lowland tropical forests" (2000: 33A). This *ad hoc* defense of such a novel hypothesis

underlines its improbability. It would be quite astonishing if eight or more species of large, mostly herding herbivore taxa had remained sequestered in southeastern Peru for six or more million years.

Recently, the assertion of Campbell et al. (2000) received minor encouragement from Ferrusquia-Villafranca (2003) on the grounds that three of the four family groups in question (†Gomphotheriidae, Tayassuidae, and Camelidae) are known in the middle Miocene of Mesoamerica. This might suggest that these three family groups could have been available for their supposed early dispersal into one corner of the Amazon Basin. Such a charitable view does not relieve those who would hypothesize a much earlier dispersal by a novel, geographic route from the need to provide more substantial evidence.

Later Features of the Interchange

After the early events of the GABI, with balanced dispersals and augmented familial diversity in both continental faunas, the evolutionary pathways of immigrant land mammals in the two American continents diverge quite dramatically. Evidently, the GABI conformed to the balanced mutual enrichment, predicted by the species equilibrium hypothesis, during the first million years, within an ecological time frame. Thereafter, however, within a more extended evolutionary time frame, the northern and southern legions embarked on radically different evolutionary pathways.

In South America, the most remarkable result of the GABI is the rapid diversification of many of the immigrants from the north. In each successive stage, the fossil record throughout the continent reflects a continual increase in the numbers of taxa derived from the first wave of immigrants. Webb and Marshall (1982: 50) quantified this trend by a census of the modern mammalian fauna at the generic level. They found that more than half (about 53%) of the present South American land mammal fauna consisted of taxa that had entered the continent by crossing the isthmian land bridge less than three million years ago.

This result becomes even more notable when one turns to the North American record and follows the very different evolutionary fate there of immigrants from South America. Little or no diversification takes place. Some genera may be considered quite successful by some measures. For example, †*Megalonyx*, a bear-sized ground sloth, evolved fairly rapidly and extended its range very widely, even reaching Alaska. However, none of the South American immigrants diversified above the species level. In the recent fauna of temperate North America, only four genera of southern immigrants survive, namely *Didelphis* L., *Dasypus* L., *Erethizon* Cuvier, and *Trichechus* L.

Why Did Northern Taxa Succeed in South America?

This striking asymmetry in the results of the GABI requires explanation. In particular, the immense success of northern immigrants in South America represents one of the greatest natural experiments in rapid evolution on a large scale. The most cogent general hypothesis may be that the northern groups that spread into South America had a long, wide-ranging history not only in North America, but also before that in Eurasia. This cosmopolitan background strongly contrasts with the long Cenozoic isolation experienced by the pre-GABI South American fauna.

A particularly intriguing part of this inequity is the presence among the northern legions of efficient mammalian carnivores. In South America, by contrast, the only mammalian carnivores were primitively modified members of the marsupial family, Borhyaenidae. The group had declined markedly before the interchange. It seems evident that the few remaining taxa could not compete with progressive carnivorans that rapidly spread into their native continent. Furthermore, the large and small herbivores of South American descent, lacking any previous experience with advanced mammalian carnivores, were overwhelmed by the rapid onslaught of wolves, jaguars, sabercats, and many smaller kinds of carnivores in the families Felidae, Canidae, and Mustelidae.

To place the GABI in a broader context, let us turn briefly to the earlier and more diffuse intercontinental interchange between Asia and North America. Table 2 lists the times and generic numbers of immigrant cohorts that entered North America from Asia. These data summarize recent tabulations for Miocene land mammals by Tedford et al. (2004). Of particular interest in this context are the several sets of immigrants that reached the New World in the middle to late Miocene. The greatest of these episodes occurred about 19 Ma (middle Miocene), when 17 Eurasian genera are recorded as new arrivals in this continent. In Woodburne and Swisher's (1995) similar codification of Cenozoic immigration events in North America, this is Interchange Event #6. Two million years later, another large wave of immigrations appeared in Interchange Event #7 (Woodburne & Swisher, 1995). A particularly important member of that cohort was †*Copemys* Wood, a probable descendant of a Eurasian murid such as †*Democricetodon* Fahlbusch. The future impact of this North American immigration event with respect to the GABI surely could not have been anticipated. Nonetheless, one epoch later, when a few inconspicuous descen-

Table 2. Miocene immigrants to North America from Asia.*

Age (Ma)	No. of genera	Selected genera**
6	7	*Lutra* (Mustelidae), †*Eocoileus* (Cervidae), †*Megantereon* (Felidae), †*Trigonictis* (Mustelidae)
7	8	*Felis* (Felidae)
8	9	†*Plionarctos* (Ursidae)
9	6	
12	2	
15	9	†*Gomphotherium* (Gomphotheriidae)
16	2	
17	11	†*Copemys* (Muridae)
19	17	
20	4	
23	6	

* Figures compiled from Tedford et al. (2004).
** See text.
† Includes both fossil and living genera.

dants of these murid rodents colonized South America, they produced by far the greatest monofamilial diversity of land mammal genera in that continent.

The next middle Miocene immigration episode introduces a taxon that is extremely far removed from murid rodents, namely, the first proboscidean in the New World. Out of Africa by way of Asia came the elephantoid genus †*Gomphotherium* Burmeister. New World descendants of this basal member of the family Gomphotheriidae diversified greatly in Central America and, following the GABI, South America.

Following a mid-Miocene lull, the late Miocene in North America witnessed another series of strong immigration episodes from Asia. New immigrant genera included the first New World deer, *Eocoileus* Webb; otters of the modern genus *Lutra* Blünnich; †*Trigonictis* Hibbard, a large extinct mustelid more or less closely related to the living tropical genus *Eira* (Hamilton) Smith (the tayra); and †*Plionarctos* Frick, the oldest known tremarctine (spectacled) bear, presumably an early sister-genus of the living Neotropical *Tremarctos* Gervais. Finally, two immigration events occurred involving the large cats: *Felis* L. and †*Megantereon* Croizet & Jobert, which is the probable antecedent of †*Smilodon* Lund, the great sabercat of the Pliocene-Pleistocene. All eight of these Miocene immigrants contributed key elements to the North American cohort during the GABI.

Evidently, these Miocene immigrants extended their ranges through the polar latitudes of the Bering Strait before climatic deterioration produced extremely cold, dry conditions. Virtually all of the omnivores, frugivores, and herbivores involved, based on reasonable interpretations of their dental adaptations and on the habits of their living relatives, required relatively mesic habitats with year-round provisions of nutritious browse, fruit, or seeds.

By the beginning of the Pliocene, the ecological valences of immigrants from Asia began to shift toward forms adapted to cold steppes. Such grazers as †*Mammuthus* Brookes, †*Bison* H. Smith, and diverse microtine rodents spread widely through most of North America but were not subsequently involved in the GABI. Evidently, they were too late to avail themselves of an open-country route through the isthmian region. There is good evidence that †*Mammuthus*, during the early Pleistocene, and †*Bison*, in the latest Pleistocene, extended their ranges southward along the relatively dry Pacific terrain into Honduras and Nicaragua. These areas today support extensive pine savannas and thorn scrub, especially along the seasonally drier Pacific slopes. Beyond that, however, these grazers did not penetrate, presumably because they were blockaded by the prevalent rainforest (Webb & Perrigo, 1984; Webb, 1997).

The purpose of this digression into Holarctic faunal movements is to show that the Bering Strait had an important effect on the GABI. Clearly, many groups of land mammals that joined the legion taxa from North America had previous evolutionary records in the World Continent. We suggest that this background may help explain their success in South America. More than two million years after the GABI, murid rodents, cervid ruminants, and other northern families with similar backgrounds burgeoned into more than half of the genera of modern South American mammals (Webb & Marshall, 1982). Wilson (1992: 130) offered the following eloquent explanation: "The World Continent ... has tested more evolutionary lines, built tougher competitors, and perfected more defenses against predators and disease. This advantage has allowed its species to win by confrontation. They have also won by insinuation: many were able to penetrate sparsely occupied niches more decisively, radiating and filling them quickly. With both confrontation and insinuation, the World Continent mammals gained the edge."

Evolutionary Patterns of Northern Interchange Taxa

To develop a full understanding of how the legions of land mammals from the north realized their full evolutionary potential in South America remains a great challenge. More than a century of dedicated paleontological spadework on both American continents has provided a reliable framework in two respects. Firstly, it has identified the set of 17 families of land mammals (Table 1). Secondly, it has de-

termined a fairly well-dated beginning point for reciprocal immigrations of legion taxa between about 3.1 and 2.7 Ma (Webb, 1985; Flynn et al., 2005).

Yet, from an evolutionary perspective, this is just the beginning of the story. The other end of the story has also been well wrought by several generations of mammalogists working out the modern systematics, ecology, and distribution of Neotropical mammal groups. Taken together, these basic facts imply some of the most dynamic examples of mammalian evolution on any continent within the entire Age of Mammals. However, most of the real phylogenetic history of these groups still remains to be told.

Presumably, the opening of a new continent after long isolation, accompanied by wholesale introduction of new kinds of mammals, provides a perfect theater for rapid, innovative evolution. The diverse nature of topographic and ecologic opportunities in South America was already evident in the mid Tertiary, especially after the uplift of the Andes (Flynn & Swisher, 1995; Burnham & Graham, 1999). This grand panorama of opportunities may have expanded even more broadly after the GABI as a consequence of increased climatic and sea level fluctuations during the Pleistocene.

The basic fossil mammal data from the late Pliocene also permit an ecological generalization about the availability of an open country route. At the time of the GABI, the isthmian region was broadly accessed by herds of grazers and browsers (Webb, 1991). The legions of the north were primarily populated by such large herbivores as horses, llamas, and deer. An especially significant role may be attributed to gomphotheres; presumably they modified the landscape by clearing trees, especially during dry seasons, much in the manner of African elephants today.

Likewise, a majority of the southern immigrant taxa reflect the same set of open landscapes. The analogy is weakened somewhat because most of the key families of large herbivores lack living relatives. Nonetheless, one can reasonably impute to toxodonts the role of rhinocerotids and confirm it with carbon isotopic data. Three or four distinct families, broadly brigaded as ground sloths, included grazers, mixed feeders, and browsers. The tank-like glyptodonts are generally perceived as herding grazers of savanna settings. In the southern set, there were also some aquatic herbivores, namely the Hydrochoeridae (capybaras) and the Trichechidae (seacows); both groups were grazers, the former arrayed along lowland waterways and the latter surely moving along the coast. In general, as emphasized by Webb (1978; 1997), the GABI data imply a broad highway of savanna and open woodland that extended from the Great Plains of North America to the Pampas of Argentina during the late Pliocene.

The most controversial part of this supposed savanna highway is the isthmian portion. In their comprehensive review of the complex late Cenozoic history of Neotropical vegetation, Burnham and Graham (1999: 560) grant that "fossil plant data are generally consistent with estimates of habitats (savannas) and climate (temperate) based on mammalian fossil faunas, but with some differences." It may be necessary to argue for the GABI savanna by calling for relatively short-lived rain shadows during the late Pliocene. GABI data do not conflict with younger evidence indicating that broad belts of rainforest probably dominated the region during most, if not all, of the Pleistocene (Colinvaux, 1997).

In South America, the remarkable radiations of northern immigrants, briefly outlined below, moved along similar ecogeographic lines. Marquet and Cofre (1999) conducted detailed analyses of South American mammal diversity partitioned into ten biomes. Their results find northern immigrant taxa dominant in the following three biomes: temperate grassland, cold winter desert, and mountain systems.

Continuing systematic studies of each of the South American phylogenetic lines promise to fill in the detailed patterns of their deployment across the continent during the Pleistocene. Molecular studies provide a particularly important set of independent evidence. Based on the degree of its generic diversification, each immigrant family may be assigned a bradytelic, horotelic, or tachytelic rate of phylogenetic evolution (Table 3). The nine bradytelic families are Soricidae, Sciuridae, Heteromyidae, Geomyidae, Leporidae, Ursidae, Gomphotheriidae, Tapiridae, and Equidae. Five of these families still consist only of the same genus that entered the continent. The four families exemplifying intermediate (horotelic) rates are Procyonidae, Felidae, Tayassuidae, and Camelidae. With nine or ten genera each, Canidae, Mustelidae, and Cervidae exemplify rapid (tachytelic) taxonomic evolution following the GABI. The fourth tachytelic family, the Muridae, exhibits truly explosive taxonomic evolution, producing dozens of genera and several tribes uniquely differentiated in South America.

The dazzling diversity of Neotropical Muridae and their interrelationships continue to challenge systematists. These field mice experienced multiple diversifications in southern deserts, in tropical lowlands, and in Andean uplands. The sense of their succcess everywhere is captured nicely by Pearson (1982: 280) in his work on small mammals of the altiplano and desert regions of Peru, wherein he cites the Muridae as "a tribute to the evolutionary ferment in South America."

Table 3. Generic diversification among northern land mammals in South America.

Family	No. of genera
Bradytelic	
Soricidae	1
Sciuridae	3
Heteromyidae	1
Geomyidae	1
Leporidae	1
Ursidae	2
†Gomphotheriidae	3
Tapiridae	1
Equidae	3
Horotelic	
Procyonidae	6
Felidae	4
Tayassuidae	4
Camelidae	5
Tachytelic	
Canidae	10
Mustelidae	9
Cervidae	9
Muridae	46–60

† Includes both fossil and living genera.

An important consideration that will increasingly concern students of phylogenetic differentiation of northern mammals in South America is the question of how much diversification had already been accomplished in tropical North America before the GABI. As noted above, the paleontological record documents that some Murid diversity (e.g., †*Prosigmodon* and †*Bensonomys*) was staged before the GABI in low latitudes of North America during the Hemphillian and Blancan (Jacobs & Lindsay, 1984). This means that molecular clock estimates of divergence times among murid rodents may date events that preceded the actual entry of those branches into South America.

Baskin (2003) recently described a surprising new example of pre-GABI differentiation: the new genus and species †*Parapotos tedfordi* Baskin representing the procyonid tribe Potosinae in the middle Miocene (Barstovian) of Texas. This taxon is the only extinct member and the first recorded fossil of the Potosinae. Without this ancient kinkajou record, it would seem reasonable to assume that modern forms developed their arboreal, nocturnal habits and their marvelous prehensile tails as post-GABI evolutionary products of their present range in multistratal rainforests of the Amazon and lowland Central America (Eisenberg, 1989).

A recent phylogenetic analysis of New World deer (Webb, 2000) documents the geographic complexity of another radiation that had been thought to be purely South American (Hershkovitz, 1982). The Andean endemics, *Hipppocamelus* Leuckart and *Pudu* Gray, are shown to be members of the tribe Rangiferini (as defined by Webb, 2000) with an extinct sister taxon, †*Navahoceros* Kurtén, in the southwestern parts of temperate North America. This tribe of mountain deer had already diverged in North America from *Mazama* Rafinesque, *Ozotoceros* Ameghino, and *Blastocerus* Gray, members of the tribe Odocoileini (as defined by Webb, 2000) before their separate southward dispersals. It seems likely that there were three or more separate entries of what are presently South American deer across the Panamanian land bridge. Thus, the issue of Central American diversification and staging of northern groups must be considered in phylogenetic analyses of South American immigrant groups.

A Southern Success Story within the American Tropics

The great success of the northern immigrants in South America has been well documented by paleontologists working in Andean localities, Argentina, and other parts of temperate South America. Those efforts, however, largely miss the contrary success story in which Central America was conquered by the tropical fauna of South America. A few sites in tropical parts of South and Central America must be more intensely developed before the full paleontological perspective can elaborate on this tropical counterdispersal.

I like to call this episode The Central American Paradox. During the Miocene, Central America had been a southern adjunct of North America, widely and deeply separated from northern South America by the Bolivar Trough. Vertebrate fossil sites in Mexico, Honduras (Gracias Formation), El Salvador, and Panama (Cucaracha Formation) corroborate the paleogeographic data by producing no evidence of any land mammals from South America (Webb & Perrigo, 1984; Ferrusquia-Villafranca, 2003). Yet today, Central America and southern Mexico are faunistically and floristically brigaded within the Neotropical Realm. This was obvious to A. R. Wallace in his great work on biogeography (Wallace, 1876). In that classic synthesis, he extended the Neotropical Realm from its major center in Amazonia up to about the Tropic of Cancer. The predominant groups of mammals in Central America today had their origins in Amazonia before the establishment of the land bridge. These were stalwart members of the ancient isolated fauna, including a diversity of New World monkeys; edentates, such as armadillos, anteaters, and sloths; and hystricognath rodents.

Unfortunately, the critical, transitional phases of this Neotropical success story are nearly opaque to paleontologists. In essence, one can study only the

Figure 4. Paleontological excavations by Universidade Federal do Acre party, led by Dr. Alceu Rancy, on Rio do Acre in late Cenozoic sediments. Photo by author.

Miocene, which is too early, or the modern fauna, which, in some sense, is too late. It is a problem familiar to any paleontologist who has attempted to overcome the refractory nature of the fossil record in tropical settings. The pressing need in this case is to redouble our efforts in primary field work in Pliocene-Pleistocene exposures throughout tropical America. Ultimately, this challenge will be answered and this mystery will yield to such ongoing endeavors as those of Laurito et al. (1993) in Costa Rica and Rancy in the western Amazon (Webb & Rancy, 1996). Figure 4 illustrates one of the valuable late Cenozoic localities on the Rio do Acre, Brazil accessible during the dry season.

Conclusions

The causes of the GABI can be traced readily and powerfully to the forces of plate tectonics in lower Central America. Hundreds of cubic kilometers of ignimbrites and other massive volcanic productions had already greatly augmented the volume of nuclear Central America during the middle Miocene. The gradual shallowing of seaways in the isthmian region, driven by persistent subduction of oceanic crust by Pacific plates, had major consequences well before the final emplacement of a continuous land bridge (Cronin & Dowsett, 1996). Jones and Hasson (1985) reviewed the many studies that demonstrate the separation and divergence of marine faunas on both sides of the isthmus. In general, deepwater species undergo geminate speciation earlier than shallow-water forms, and such patterns can be demonstrated in many organisms both across a broad range of taxonomic levels and also by rapidly diverging molecular systems, notably by mitochndrial DNA (Collins, 1996). Rapid divergence between Atlantic and Pacific descendants of planktonic foraminifera, such as the globigerinid †*Globorotalia multicamerata*, indicates that the seaway was breaking up between about 3.6 to 3.1 Ma. The importance of this process in reorganizing oceanographic currents and intensifying the Gulf Stream was indicated by Keigwin (1982) and Cronin and Dowsett (1996), who also noted its probable role in generating northern hemisphere ice sheets beginning about 3.2 Ma and again around 2 Ma.

The final emplacement of a continuous isthmian land bridge is faithfully recorded by the appearance of legions of land vertebrates reciprocally dispersing between North and South America. Substantial evidence from long sections in temperate latitudes of both continents places the GABI events between about 2.7 and 3.1 Ma (Webb, 1985; Flynn et al., 2005).

During the first million years or so of the GABI, the contribution of each continent to the faunal in-

terchange was roughly equal at the family level, and each continental fauna was taxonomically enriched. Subsequently, by early Pleistocene time, the interchange, as recorded by new immigrants, was essentially completed and family-group diversities had dropped back to previous levels, in accord with predictions of species equilibrium theory.

The northern legion taxa experienced astonishing evolutionary success as measured in the modern South American fauna, capturing more than half of the present generic diversity. When that broad record is partitioned, it is seen that nine families simply entered the continent with little or no taxonomic diversification above the species level (cf. Table 3, bradytelic families). Four other families of northern land mammals evolved taxonomically at moderate (horotelic) rates: these include Procyonidae, Felidae, Tayassuidae, and Camelidae. The four families that really seized the new opportunities in South America, evolving at tachytelic rates, were Canidae, Mustelidae, Cervidae, and especially Muridae. It is worthy of note that their success focused ecologically on the very biomes that most nearly resembled temperate biomes from whence they had come. According to Marquet and Cofre's (1999) detailed analyses of mammalian diversity in ten biomes, northern immigrant taxa are dominant in temperate grassland, cold winter desert, and mountain systems.

A countervailing conquest of Central America by the Amazonian biota, while nearly opaque to paleontologists, has been fully appreciated by most biologists since Alfred Russell Wallace (1876) proposed the Neotropical Realm. There are hints in the relatively weak tropical portions of the vertebrate fossil record that this phase of the GABI came after the Pliocene and that during the Pleistocene the Panamanian land bridge was more fully occupied by rainforest (Webb, 1991; Webb & Rancy, 1996). Paleobotanical evidence makes a strong case for this (Colinvaux, 1997; Burnham & Graham, 1999).

Among land mammals, the prominent protagonists in this second phase, into Central America, were old southern taxa including marsupials, primates, xenarthrans (both cingulates and pilosans), and hystricognath rodents. It is not surprising that these same old southern taxa outnumber the northern newcomers in the two South American biomes designated by Marquet and Cofre (1999) as temperate rain forest and tropical humid forest.

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LATE QUATERNARY ENVIRONMENTS OF THE NORTHERN DESERTS AND CENTRAL TRANSVOLCANIC BELT OF MEXICO[1]

Sarah E. Metcalfe[2]

Abstract

The detailed nature of climatic change over the late Quaternary remains poorly understood for northern and central Mexico. A scarcity of records in the former and great complexity in the latter have hindered a thorough reconstruction of changing environments. Previously published research by Metcalfe et al. highlighted questions relating to conditions at the last glacial maximum (LGM), the nature of the transition from glacial to interglacial conditions, and change over the Holocene, including the role of phenomena such as El Niño–Southern Oscillation (ENSO). Here, data from the Sonoran Desert, the Chihuahuan Desert, and the Trans-Mexican Volcanic Belt (TMVB) (and adjacent oceans) are reviewed. In the desert regions, the mid-Pleistocene may have been drier than the late Pleistocene, which was significantly cooler than present and saw more winter precipitation derived from midlatitude frontal systems. There was a significant expansion southward of woodland taxa, although many fossil vegetation assemblages apparently have no modern analogues. Extensive paleolakes existed in the modern desert. Conditions wetter than present persisted into the Holocene, but the modern summer rainfall regime may not have become established until after 9000 uncalibrated radiocarbon-dated years before present (^{14}C yr. BP). Fully modern conditions started about 4000 ^{14}C yr. BP. In the TMVB, sparse lake sediment records indicate that the mid-Pleistocene may have been wetter than the late Pleistocene. Further data are still required to confirm whether the proposed pattern of a wet west and a dry east around the LGM holds true. Most lake sediment records show major anthropogenic influence from the mid-Holocene on, although there is evidence for increasing climatic variability in the late Holocene. New deep sea core records indicate the glacial meltwater was re-routed into the Gulf of Mexico after the Younger Dryas cool event, helping to explain the delayed onset of the modern summer rainfall pattern in relation to general warming. High-resolution records are still confined to deep sea cores and tree rings, but highlight the region's vulnerability to climatic change.

Keywords: Chihuahua, climate change, late Quaternary, Mexico, Sonora, Trans-Mexican Volcanic Belt.

Resumen

La naturaleza detallada del cambio climático durante el Cuaternario tardío en el norte y centro de México es aún poco entendida. La escasez de registros en el primero y la complejidad del segundo, han dificultado una reconstrucción detallada de ambientes cambiantes. La investigación previamente publicada por Metcalfe et al. destaca preguntas relacionadas a las condiciones durante la máxima de último glacial (LGM), la naturaleza de la transición de glacial a las condiciones interglaciales, y de cambio durante el Holoceno, incluyendo el papel de fenómenos tales como El Niño–oscilación meridional (ENSO). Aquí se revisan los datos del desierto de Sonora, el desierto de Chihuahua y el cinturón volcánico trans-mexicano (TMVB) (y los océanos adyacentes). En las regiones desérticas, el Pleistoceno medio pudo haber sido más seco que el Pleistoceno tardío, que fue significativamente más frío que el presente y tuvo más precipitación invernal derivada de sistemas frontales de latitudes medias. Hubo una expansión significativa de taxones leñosos hacia el sur, aunque muchos grupos fósiles de vegetación al parecer no tienen ningún análogo moderno. Paleolagos extensos existieron en el desierto moderno. Condiciones más húmedas que las actuales persistieron en el Holoceno, pero el régimen de lluvias de verano moderno pudo no haberse establecido hasta después 9000 años de radiocarbono no calibrados antes del presente (^{14}C yr. BP). Condiciones completamente modernas comenzaron cerca de 4000 ^{14}C yr. BP. En el TMVB, escasos registros de sedimentos lacustres indican que el Pleistoceno medio pudo haber sido más húmedo que el Pleistoceno tardío. Todavía se requieren datos adicionales para confirmar si el propuesto patrón de un oeste húmedo y un este seco alrededor del LGM es verdadero. La mayoría de registros lacustres demuestran una importante influencia antropogénica desde mediados del Holoceno hacia adelante, aunque hay evidencia de un aumento en la variabilidad climática en el Holoceno tardío. Los registros profundos del fondo del mar indican que el aguanieve glacial fue reencaminada hacia el golfo de México después del evento del enfriamiento del joven Dryas, lo que ayuda a explicar el inicio retrasado del patrón moderno de la precipitación de verano en relación al calentamiento general. Registros de alta resolución todavía se confinan a muestras del fondo del mar y a anillos de árboles, pero destacan la vulnerabilidad de la región a los cambios climáticos.

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The late Quaternary saw the transition from a glacial climate (with the global glacial maximum at 18,000 uncalibrated radiocarbon-dated years before present (^{14}C yr. BP)) into the modern interglacial climate at about 10,000 ^{14}C yr. BP. Although the broad patterns of climatic change over this period in tropical and sub-tropical areas have been identified (e.g., Gasse, 2000), the detailed nature of change remains poorly understood. This is particularly true for northern and central Mexico. Records from northern Mexico, especially terrestrial records, are scarce, and in central Mexico the complexity of the environment has hindered making climatic reconstructions. In practice, most records are also confined to the past 70,000 years or so (the mid-Pleistocene ca. 70,000–45,000 before present (BP), equivalent to marine isotope stage 3).

Global climatic change during the Pleistocene and Holocene brought about major changes in precipitation regimes (amount and seasonality), as well as changes in temperature and sea level. In general, the glacial world was drier than the interglacial world, but there are regional variations to this pattern. The area to the southwest of the Laurentide ice sheet, including present day northern Mexico, was one area of increased moisture availability around the LGM (COHMAP Members, 1988; Thompson et al., 1993). In tropical and subtropical areas, moisture availability is a key aspect of climatic change, bringing about major shifts in drainage systems and vegetation distributions.

The nature of climatic and environmental change can be reconstructed using a range of sources, or proxies. Most of these proxies provide records of relatively low temporal resolution (e.g., decadal, centennial) depending on the rate at which material accumulates. Key sources of low-resolution data are lake cores, ocean cores, glacial records, packrat middens, and paleosols. Some records, however, have annual (or even seasonal) resolution; these include some ocean cores and lake cores, ice cores, tree rings, and historical and instrumental records. This paper reviews climate records from central and northern Mexico and the adjacent oceans based on a wide range of proxies. The focus here is on records that have been published since the reviews of Metcalfe et al. (2000) and Fritz et al. (2001). The chosen study area includes the modern Sonoran and Chihuahuan deserts and the highlands of the Trans-Mexican Volcanic Belt (TMVB) (Figure 1).

The Climate of Mexico

The modern climate of Mexico is dominated by seasonal shifts in the position of the Inter-Tropical Convergence Zone (ITCZ), the position and intensity of subtropical high-pressure cells (e.g., the Bermuda-Azores High), and the frequency and extent of midlatitude westerly depressions. In winter, with the ITCZ in a southerly position (Fig. 2a), most of Mexico is dominated by high pressure, resulting in dry conditions. Cyclonic systems, originating in the Pacific Ocean, affect northwestern and central Mexico and bring frontal rainfall. A very small area of northwest Mexico (primarily the west coast of Baja California) receives most of its precipitation in winter. On the east side of Mexico, some precipitation is brought by *nortes*, cold winds originating over North America that pick up moisture over the Gulf of Mexico (Mosiño Aleman & Garcia, 1974). In summer, the ITCZ moves north, and moist, easterly flow is established over the country (Fig. 2b). This has been identified as a monsoonal-type circulation. The period June to September is the main wet season over most of Mexico. The principal source of moisture is the Gulf of Mexico, with flows extending up into the Great Plains of the United States and Canada. On the west side of Mexico, a low-level flow, called the Mexican Monsoon, becomes established, drawing moisture northward along the Pacific margin, through the Gulf of California (or Sea of Cortez), and into the southwestern United States (Douglas et al., 1993; Higgins et al., 1998). Convective storms and tropical storms (originating over both the Pacific Ocean and Gulf of Mexico/Atlantic Ocean) make a significant contribution to summer precipitation (e.g., Englehart & Douglas, 2001).

The position and strength of the key features influencing pressure distributions and, hence, precipitation are known to be affected by climatic phenomena such as El Niño–Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO), and the Pacific Decadal Oscillation (PDO). Although the effects of ENSO are complex in this region, in broad terms El Niño years see increased winter precipitation in northwest Mexico and drier summers overall (Magaña et al., 2003), while La Niña years result in more summer precipitation.

Across the whole of Mexico, both precipitation and temperature are strongly affected by altitude and aspect (Fig. 3a). The highlands of the TMVB, which cross Mexico at about 19°N (Fig. 1), have a remarkably temperate climate because much of the land lies above 2000 m, with the highest peaks reaching more than 5000 m and supporting permanent ice cover. Pine and oak forests are the dominant natural vegetation over most of the TMVB. In northern Mexico, the highlands of the Sierra Madre Oriental and Occidental are similar to the TMVB (Fig. 3b). The plateau area between these ranges (the Mesa Central)

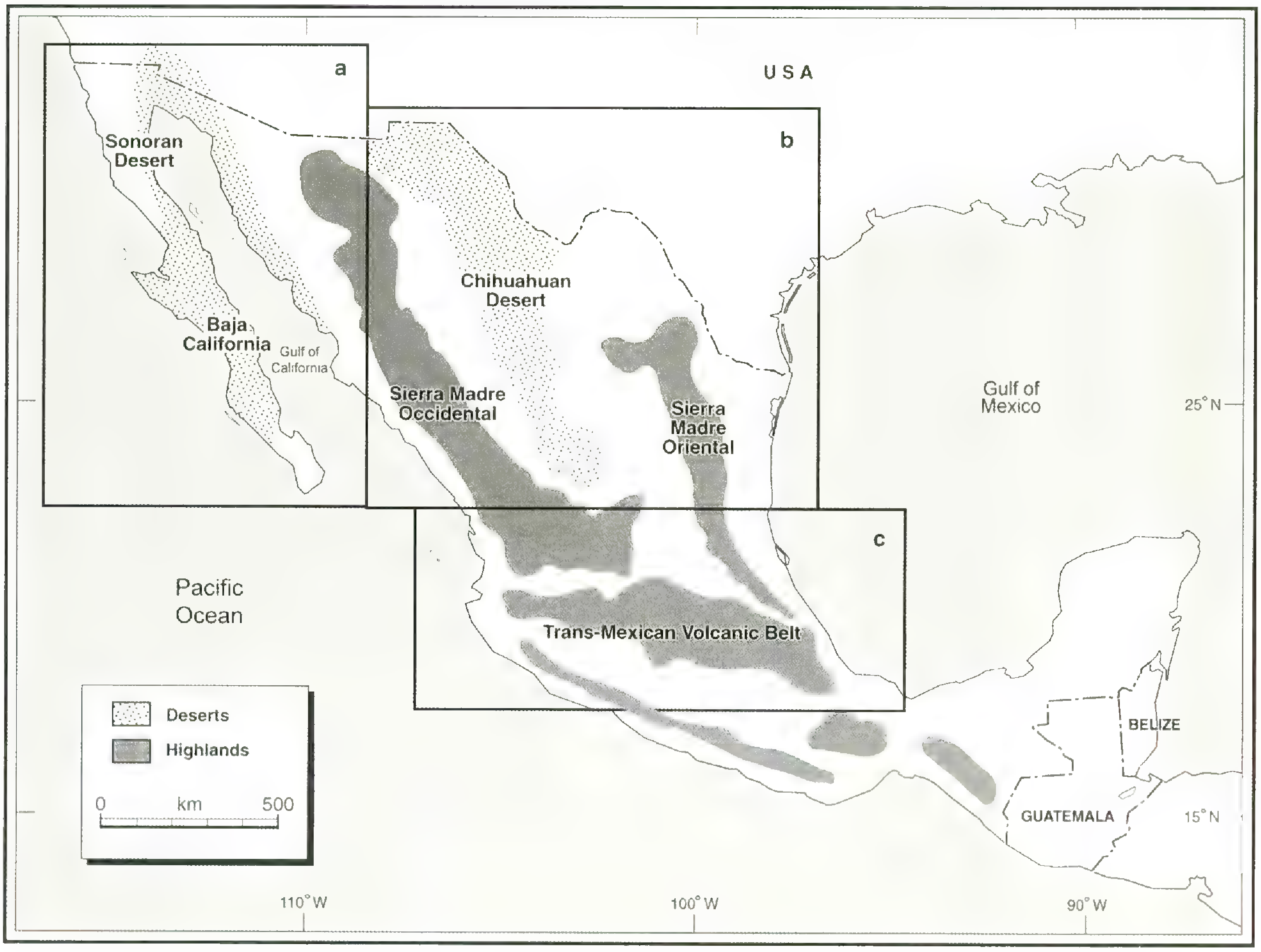

Figure 1. Main topographical features of Mexico showing the locations of the study areas. —a. Baja/Sonora. —b. Chihuahua. —c. Trans-Mexican Volcanic Belt.

declines in elevation northward toward the modern Mexico–U.S.A. border. Lower altitudes, the increasing predominance of subtropical high pressure, and distance from moisture sources give rise to the Chihuahuan Desert. Annual precipitation in the border area is about 200 mm, and there are areas of active dunes. The vegetation of the modern Chihuahuan lowlands is dominated by creosote bush (*Larrea tridentata* (Sessé & Moçiño ex DC.) Coville), with a range of other shrubs; yuccas, especially soaptree yucca (*Yucca elata* (Engelm.) Engelm.); agaves; cacti; and grasses. In northwestern Mexico, dry conditions are exacerbated by the occurrence off-shore of the cold California current. Areas of Baja California and Sonora are the driest in Mexico, with less than 100 mm of rain annually (Fig. 3a). This broad area lies within the Sonoran Desert. Here a summer rainfall maximum is the norm, except for parts of Baja California and coastal Sonora that are exposed to winter frontal systems (see above). Although creosote bush occurs in the Mexican part of the Sonoran Desert, it is not as abundant as it is farther north. Lowland vegetation includes many forms of cacti, yuccas, agaves, and forms of ocotillo, including the boojum tree (*Fouquieria columnaris* (Kellogg) Kellogg ex Curran). Rzedowski (1973) has highlighted the diversity of vegetation in Mexican dryland areas and the distinct differences between the Chihuahuan and Sonoran floras.

Baja/Sonora

Today, this area of northwest Mexico (Fig. 1) is extremely dry (see above), and the range of terrestrial sites that have preserved paleoclimatic records is very limited. Sources of paleoclimatic data include tree rings, packrat middens, lake sediments, and deep sea cores (Fig. 4). Although tree ring records from this area extend back into the 15th century, there are no other proxy records for comparison, and no attempt has been made to relate the tree ring records to archival records. As a result, the tree ring data will not be discussed here.

Most of the paleoclimate data for this region comes from packrat (*Neotoma* Say & Ord) middens. Packrat middens preserve plant macrofossil remains, which allow reconstruction of local vegetation to species level. They may also contain pollen, which allows

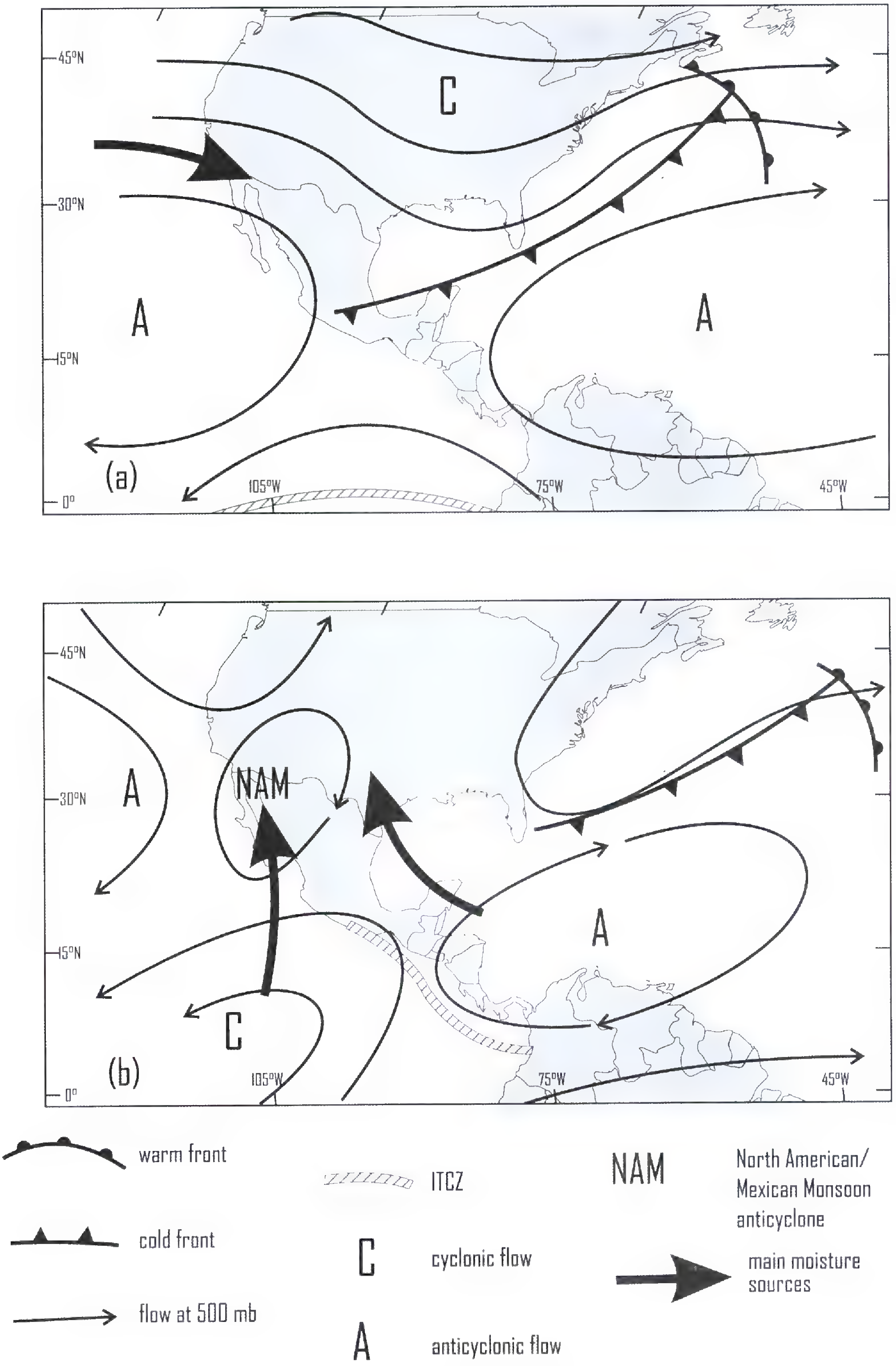

Figure 2. Main features of the atmospheric circulation across Mexico. —a. In winter. —b. In summer. ITCZ = Intertropical Convergence Zone. Redrawn after Metcalfe et al. (2000).

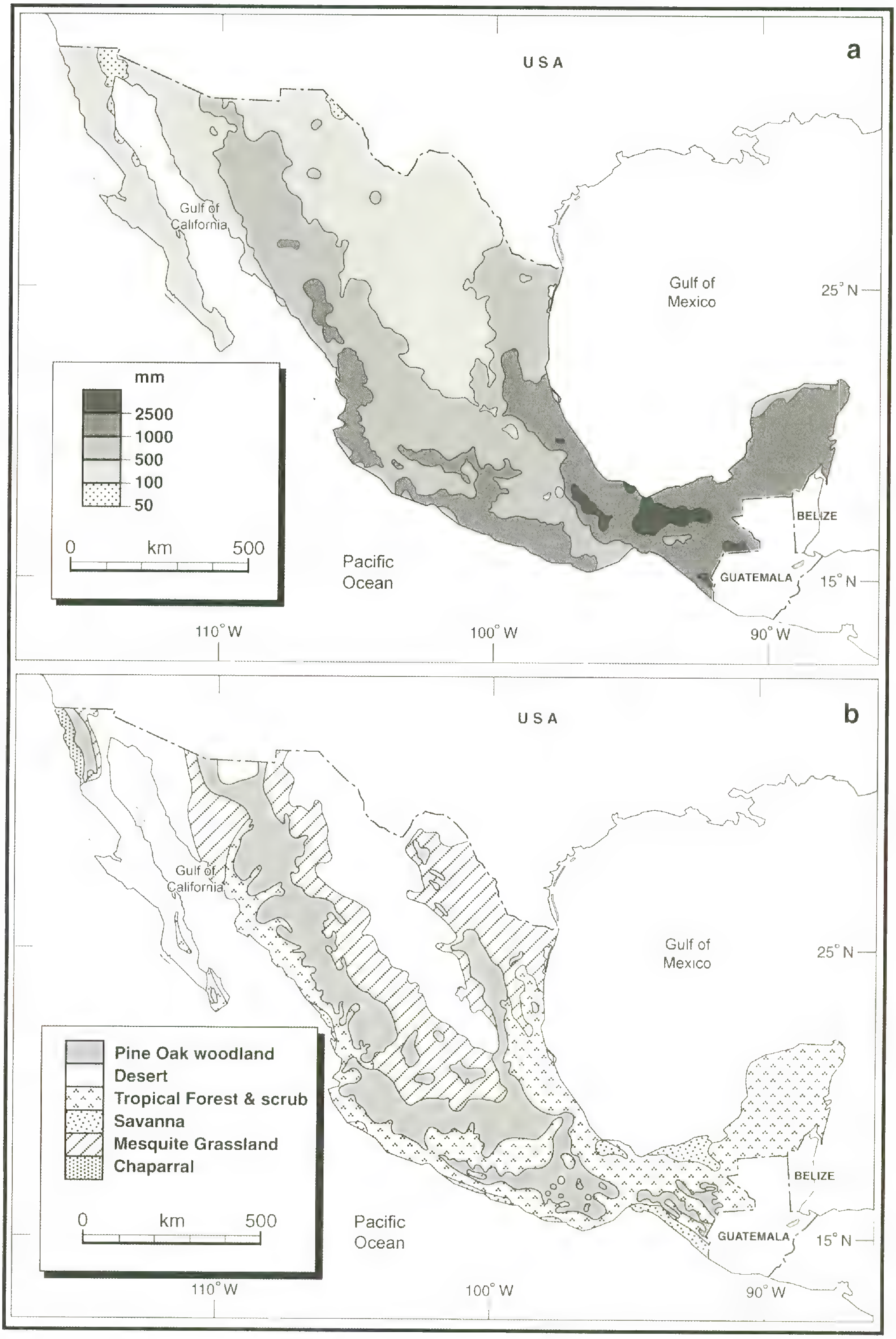

Figure 3. —a. Total annual precipitation, —b. Major vegetation types across Mexico. (a, based on data for 1941–2002 from the Servicio Meteorológico Nacional, Mexico; b, based on data from the Instituto Nacional de Estadística, Geografía e Informatica, and Rzedowski (1994)).

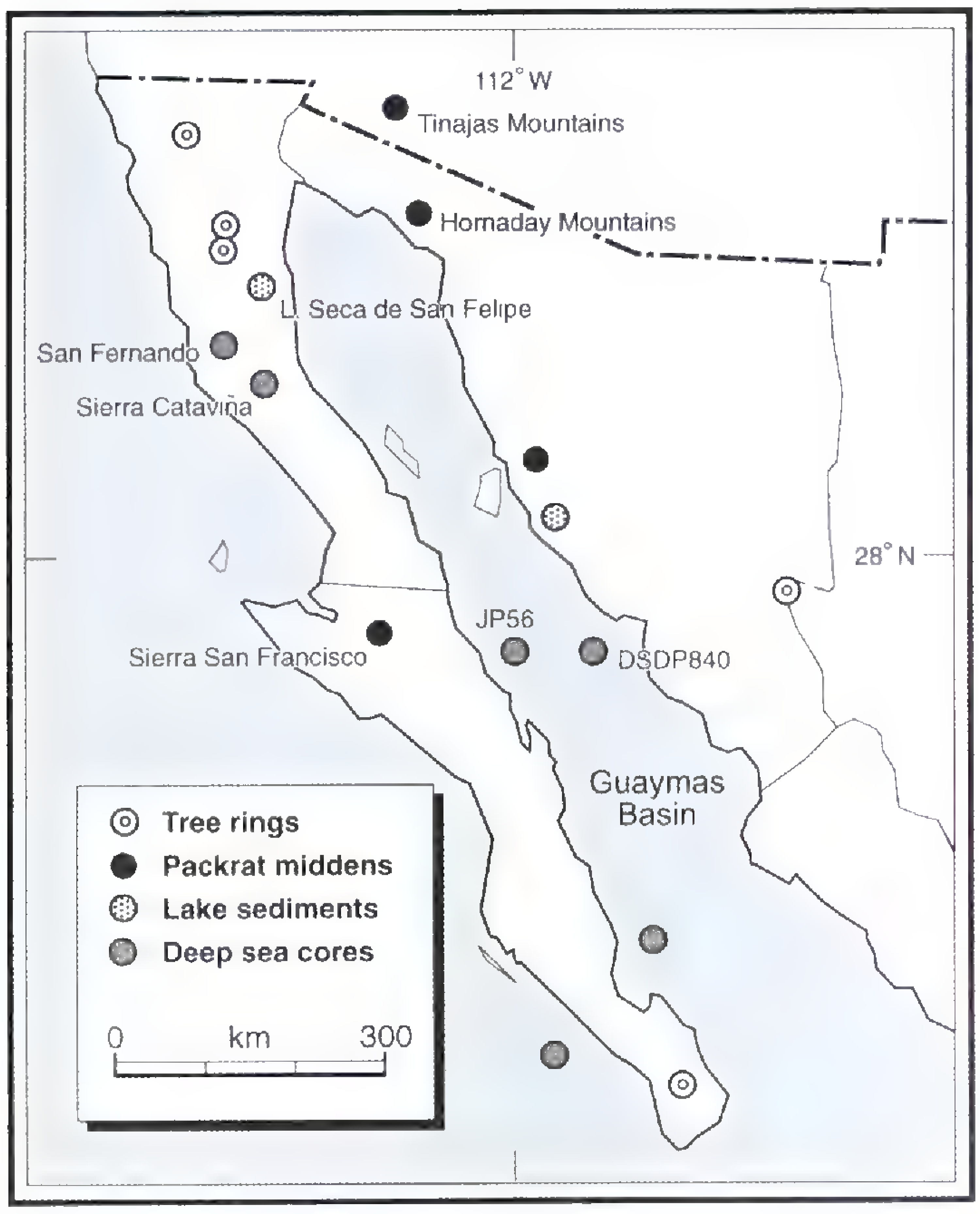

Figure 4. Sources of paleoclimatic data for the Baja/ Sonora region. Sites referred to in the text are named.

reconstruction of both regional and local vegetation (Anderson & Van Devender, 1995), but only to generic or family level. Species-level identification of paleovegetation is an asset to reconstructing climate, because it can be used to identify the season of precipitation; this is a key concern in both Baja/ Sonora and Chihuahua. The longest midden records from Baja California (Sierra Cataviña and San Fernando) extend back ca. 30,000 years (Van Devender, 1990a; Peñalba & Van Devender, 1997; Van Devender, 1997), while a record from the Tinajas Mountains (just over the border in Arizona) reaches back to 43,000 BP (Van Devender, 1990a). Although the amount of data is limited, it appears that in this area the mid-Pleistocene may have been drier than the late Pleistocene (Van Devender, 1990a). The mid-Pleistocene middens from Tinajas include Joshua tree (*Yucca brevifolia* Engelmann), a Mojave desert species that is not found in the late Pleistocene middens. In contrast, single leaf pinyon (*Pinus monophylla* Torrey & Fremont), although present, is more common in the late Pleistocene. The late Pleistocene (full glacial, equivalent to marine isotope stage 2) seems to have been significantly cooler than present (by 5° to 6°C), with more winter precipitation. Pinyon (e.g., Parry pinyon (*Pinus quadrifolia* Parlatore ex Sibworth)), juniper (e.g., western juniper (*Juniperus occidentalis* Hooker)), and chaparral species were present more than 400 km south of their present day distributions in southern California and northern Baja California. A record from the Sierra San Francisco (Rhode, 2002), 300 km south of Sierra Cataviña (Fig. 4), which is today vegetated with scrub and succulents, confirms the southward expansion of juniper and chaparral vegetation even at relatively low elevations (< 800 m). Based on the modern distribution of California juniper (*Juniperus californica* Carrière) and other taxa, this area of central Baja California may have experienced a mild, Mediterranean climate in the late Pleistocene and early Holocene, with at least twice as much winter precipitation as it receives today.

It is interesting to note that many of the late Pleistocene vegetation communities recorded in the middens have no complete modern analogues. This may indicate that although the late Pleistocene climate here was similar to that of present day southern California, there were some differences. Woodland plants apparently persisted in this area into the early Holocene (at least at elevations above 250 m). Cooler summers and greater winter precipitation seem to have continued. Middens from the Hornoday Mountains in northwest Sonora, close to the Gran Desierto, however, do not show the woodland plants found in other Sonoran Desert sites at this time. From about 9000 ^{14}C yr. BP, the winter rainfall regime seems to have collapsed and the modern, summer rainfall–dominated climate regime became established. Pinyon-juniper-oak woodland, with chaparral species, were replaced by juniper-oak chaparral and, finally, by Sonoran desert scrub (Van Devender, 1997).

The middle Holocene was warmer and generally wetter than present (more summer rain). Middens from Cataviña, however, show that woodland and chaparral elements had died out and been replaced by mesquite (*Prosopis* sp.) and then cactus (Van Devender, 1997). An increasing abundance of C_4 grasses is often taken as being indicative of more summer rainfall, although their interpretation in the fossil record has been disputed (Van Devender et al., 1990; Holmgren et al., 2003). McAuliffe and Van Devender (1998) report that frost-intolerant taxa were present in the northern Sonoran Desert and suggest that temperatures in the early to mid-Holocene were 2°C warmer than present. They also point out that more frequent tropical cyclones may have contributed to increased overall precipitation levels. These mid-Holocene conditions are consistent with insolation changes driven by Milankovitch forcing. The present day vegetation of Sonoran desert scrub and cactus seems to have been established about 4000 BP.

Lake sediment records from Baja/Sonora are extremely scarce. There are paleolake basins, but

poor microfossil preservation and difficulties with obtaining a reliable chronology have severely limited the usefulness of those that have been studied. The best dated record comes from the Laguna Seca San Felipe in Baja California (Ortega et al., 1999; Lozano García et al., 2002), with a core covering the period from about 70,000 to 4000 ^{14}C yr. BP. The sequence indicates a relatively dry mid-Pleistocene followed by a wetter late Pleistocene. The pollen record indicates the presence of open pine and juniper woodland in the mid-Pleistocene, with an expansion of juniper woodlands in the late Pleistocene. Strong summer cooling and increased winter precipitation are proposed as the most likely explanation for the observed changes in vegetation. Planktonic, saline water diatoms are present for the period from 34,000 to 28,000 BP, and lacustrine conditions seem to have persisted until about 12,000 BP. There is some suggestion that the Younger Dryas (11,000 to 10,000 ^{14}C yr. BP) was dry but that conditions wetter than present marked the early Holocene through to 7000 BP. No pollen record was preserved in these sediments. Aeolian sediments mark drying in the mid-Holocene, and about the last 4000 years of the record seem to have been lost. Although the record from Laguna Seca has a number of problems, it does seem to be remarkably consistent with that derived from the much more abundant midden data.

Unlike the terrestrial environment, conditions in the Gulf of California (Fig. 1) are conducive to well-preserved and high-resolution paleoclimate records. A large number of deep sea cores have been retrieved from this area, particularly from the Guaymas Basin. High productivity and anoxic conditions at depth have resulted in the deposition of laminated sediments giving the potential for seasonal resolution (Pike & Kemp, 1997). There are periods of non-laminated (massive) sedimentation, such as during the full glacial and Younger Dryas periods. Despite these promising conditions, the interpretation of records from the Gulf of California is far from straightforward. Sancetta (1995) reported results from core JP56 (western Guaymas Basin, Fig. 4) that suggested weak westerly winds in the late glacial and Younger Dryas periods, but more El Niño–like conditions and an increase in westerly winds into the early Holocene. This pattern of change is quite inconsistent with that derived from terrestrial records (in Baja/Sonora and the nearby southwest U.S.A.) and with modelling results. By the mid-Holocene, however, the record from JP56 is consistent with terrestrial records as modern conditions are indicated.

A more recent record (Barron et al., 2004) from the eastern Guaymas Basin (core DSDP 840) has highlighted the difficulties of matching marine and terrestrial records in the late Pleistocene. The authors use percent weight $CaCO_3$ as an indicator of tropical ocean influence. High percentages in the late glacial and Younger Dryas periods seem to indicate warm conditions, and the Younger Dryas sediments also have a higher number of tropical diatom species. The straightforward interpretation of the Younger Dryas sediments is that they reflect the persistence of tropical ocean influence (today a summer and autumn phenomenon). However, the authors note that this apparent warmth is inconsistent with both the midden data (see above) and the results from deep sea cores taken farther north in the Santa Barbara Basin and elsewhere off the California coast. The DSDP 840 core shows an abrupt change in the early Holocene, with an increase in productivity. Cooler and more saline conditions in the early to mid-Holocene are explained as being due to intensified northwest winds; however, this is difficult to reconcile with the terrestrial records. A spike in productivity at 8200 BP (ca. 7400 ^{14}C yr. BP) is attributed to a cold event in the North Atlantic brought about by the catastrophic drainage of Lake Agassiz. This cold event (also seen in the Greenland GISP2 ice core) apparently resulted in stronger westerlies and more upwelling, driving an increase in productivity. Around approximately 6200 BP (5400 ^{14}C yr. BP), the core record shows the onset of modern ENSO conditions, which have occurred with increasing frequency over the last 3000 years. Unfortunately, there are no long terrestrial ENSO records for comparison, but the onset of the modern ENSO regime about 5000 BP has been reported elsewhere (Rodbell et al., 1999; Tudhope et al., 2001; Moy et al., 2002).

Over shorter timescales, ENSO records are preserved in tree rings (Stahle & Cleaveland, 1993). In this area, tree growth appears to be responsive to increased winter precipitation during El Niño events (although summers are dry). The PDO shows ENSO-type features over longer time scales, with warm (positive) phases being El Niño–like (eastern Pacific warm) and cool (negative) phases being La Niña–like (eastern Pacific cool) (Higgins et al., 2003). Evidence for low frequency variability (40-year and 80-year cycles) consistent with the PDO has been found by combining tree ring and reconstructed streamflow data from the Gulf of California watershed (Brito Castillo et al., 2003).

Chihuahua

This area is taken to include the Mexican part of the Chihuahuan Desert, covering the modern states of Chihuahua, Coahuila, Durango, northern Zacatecas, and parts of Nuevo Leon and Tamaulipas (Fig. 1). As

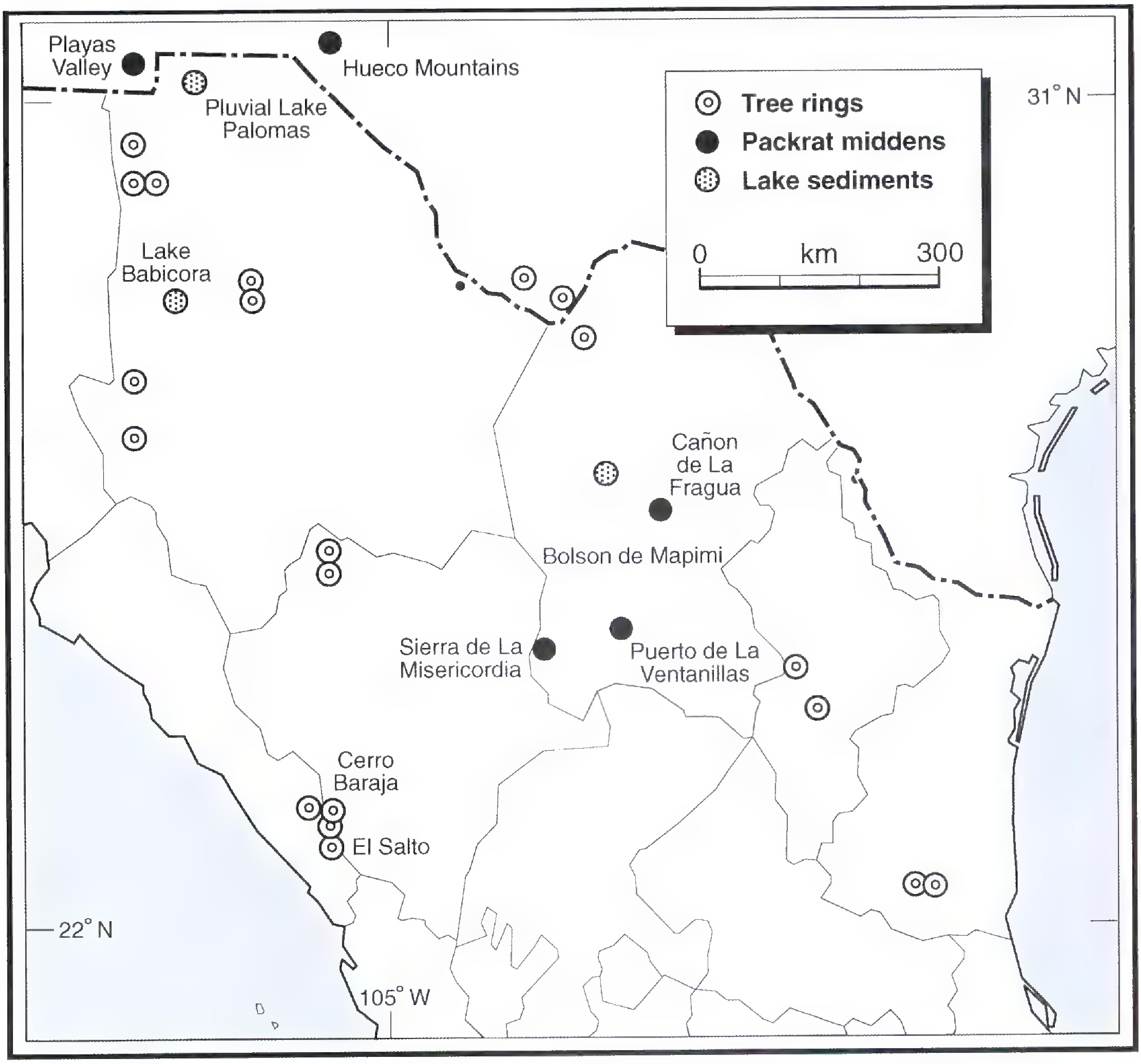

Figure 5. Sources of paleoclimatic data for the Chihuahua region. Sites referred to in the text are named.

described above, summer rainfall predominates here, with strong altitudinal and latitudinal gradients. As in Baja/Sonora, key paleoclimatic data for the Chihuahuan area (Fig. 5) have come from packrat middens, although there are few records for the Mexican part of the Chihuahuan Desert compared with the part within the U.S.A. Middens from the Hueco Mountains (west Texas, Fig. 5) provide a record covering about 42,000 years (Van Devender, 1990b). These record the presence of woodlands with sandpaper bush and big sagebrush (*Artemisia tridentata* Nuttall type) in the mid-Pleistocene. Sandpaper bush and big sagebrush are generally considered to be Great Basin plants; their presence indicates that their range extended southward in this period. They are only rarely present in late Pleistocene and Holocene middens. There are three records from the Bolson de Mapimi (Coahuila) that cover about the last 13,000 years (Van Devender & Burgess, 1985). These show that in the late glacial period, the vegetation of the area was a woodland of juniper and papershell pinyon (*Pinus remota* (Little) L. H. Bailey & Hawksworth), but that these were replaced by Chihuahuan desert scrub and succulents between 12,000 and 9000 ^{14}C yr. BP. This change from woodland to scrubland vegetation occurred earlier here than in Baja/Sonora.

By including midden data from the whole of the Chihuahuan Desert (e.g., Betancourt et al., 2001; Holmgren et al., 2003), a longer and more complete record of climatic change can be obtained. In the Chihuahuan Desert, it appears that the mid-Pleistocene was drier than the late Pleistocene only at the lowest elevations (cf. Baja/Sonora). The late Pleistocene was marked by cooler summers and mild, wet winters, but it seems that there was still some summer rainfall (shown by C_4 grasses and summer annuals).

These wetter conditions resulted in an expansion of pinyon-juniper woodland, including papershell pinyon and Colorado pinyon (*P. edulis* Engelmann), as far south as 26°N. As in Baja/Sonora, there are no modern analogues for some of these late Pleistocene communities, particularly those in modern New Mexico.

In the early Holocene, winters still seem to have been wetter than present, although the limit of winter rainfall was apparently tracking northward by 9000 BP. The modern climatic regime was established between 9000 and 8000 BP as desert shrubs replaced the woodland taxa (except at high elevations). It has been noted that some vegetation types responded very rapidly to increasing summer temperatures and precipitation. Conditions wetter than present apparently persisted through the early Holocene, driven by summer (monsoonal) rain, although midden records are quite scarce. Holmgren et al. (2003) explain the lack of mid-Holocene (8000 to 4000 BP) middens in the Playas Valley (southwestern New Mexico, in the U.S.A.–Mexico border area) as being due to persistent winter drought that led to a decline in woody perennials. As in Baja/Sonora, modern conditions seem to have set in about 4000 BP with the arrival of desert scrub species including creosote bush.

As in the Sonoran Desert region, lake sediment records in Chihuahua are few and microfossil preservation is often poor. There does, however, seem to be much more potential for records from the Chihuahuan area because it is the southward extension of the Basin and Range province and because there are extensive paleolake basins. The earliest work in the area was a pollen record from the Bolson de Mapimi published by Meyer (1973). This apparently showed little change in vegetation (and hence climate), although the midden data from the same area contradict this. More recent records have come from farther north and confirm that the area has experienced significant climatic change over the late Quaternary. The Babicora Basin, at 2200 m in the foothills of the Sierra Madre Occidental (Fig. 5), has been the focus of most work (Metcalfe et al., 2002; Ortega Ramirez et al., 1998; Palacios-Fest et al., 2002). Cores from the basin floor and sections from the basin margins have provided a record covering about the last 65,000 years. Diatom, pollen, and geochemical data show that an extensive lake occupied the Babicora Basin throughout the mid- to late Pleistocene and into the early Holocene. The diatom record shows strong fluctuations in conditions in the mid-Pleistocene (with a period of enhanced evaporation) that are consistent with the midden data. Cool conditions around the LGM are indicated by the presence of forests of fir (*Picea* A. Dietrich) and pine. It is clear from the Babicora record and from lake level records elsewhere in the Great Basin that the dry conditions of the late Holocene are very unusual. The increased moisture availability across this area in the middle and late Pleistocene is thought to be the result of increased winter precipitation (Bradbury et al., 2000). The Holocene record from Babicora is rather patchy, particularly from the cores. A change in dominant diatom taxa in the early Holocene is thought to indicate a shift to summer precipitation (Metcalfe et al., 2002). A permanent lake seems to have persisted into the mid-Holocene, but with strong variability in water level (Ortega Ramirez et al., 1998). Dry conditions are indicated around 5000 BP. An analysis of Mg/Ca ratios in ostracods (Palacios-Fest et al., 2002) from the late Holocene (after 4000 BP) has been interpreted as indicating colder winters with more effective moisture, possibly more winter precipitation. This would be consistent with the southward shift of the ITCZ from the mid-Holocene (see below), making summer precipitation less dominant.

A more detailed Holocene record has been published for lakes El Fresnal and Santa Maria a little farther north of Babicora (Castiglia & Fawcett, 2001, 2006). These basins were part of Pleistocene paleolake Palomas (Fig. 5), but Castiglia and Fawcett (2001, 2006) report the occurrence of large lakes in the Holocene, including the Little Ice Age. The largest Holocene lake seems to have been present around 8000 BP and covered more than 5600 km^2. The mid-Holocene showed high variability, with a reasonably extensive lake in 6000 and 4000 BP, but with dry conditions at 5000 BP. The authors suggest that millennial-scale high stands may be linked to Bond cycles in the North Atlantic and that the Holocene high stands may reflect increased winter precipitation associated with increasing El Niño events (see above).

Consideration of all the published terrestrial long-term climate records from northern Mexico and adjacent areas yields a very consistent picture of change since the mid-Pleistocene. The Pleistocene was cooler than present (up to 5° to 6°C around the LGM) and generally wetter, with the mid-Pleistocene drier than the late Pleistocene. Pinyon and juniper woodland extended over substantial areas of what are now the Chihuahuan and Sonoran deserts, and chaparral vegetation extended into southern Baja California. Some of the vegetation communites recorded in packrat middens have no modern analogues. Extensive lakes and wetlands occupied basins in present day Chihuahua and Coahuila. The data seem to support previous explanations that wetter conditions were driven by increased winter precipitation originating over the Pacific Ocean and driven southward by the mass of the Laurentide ice

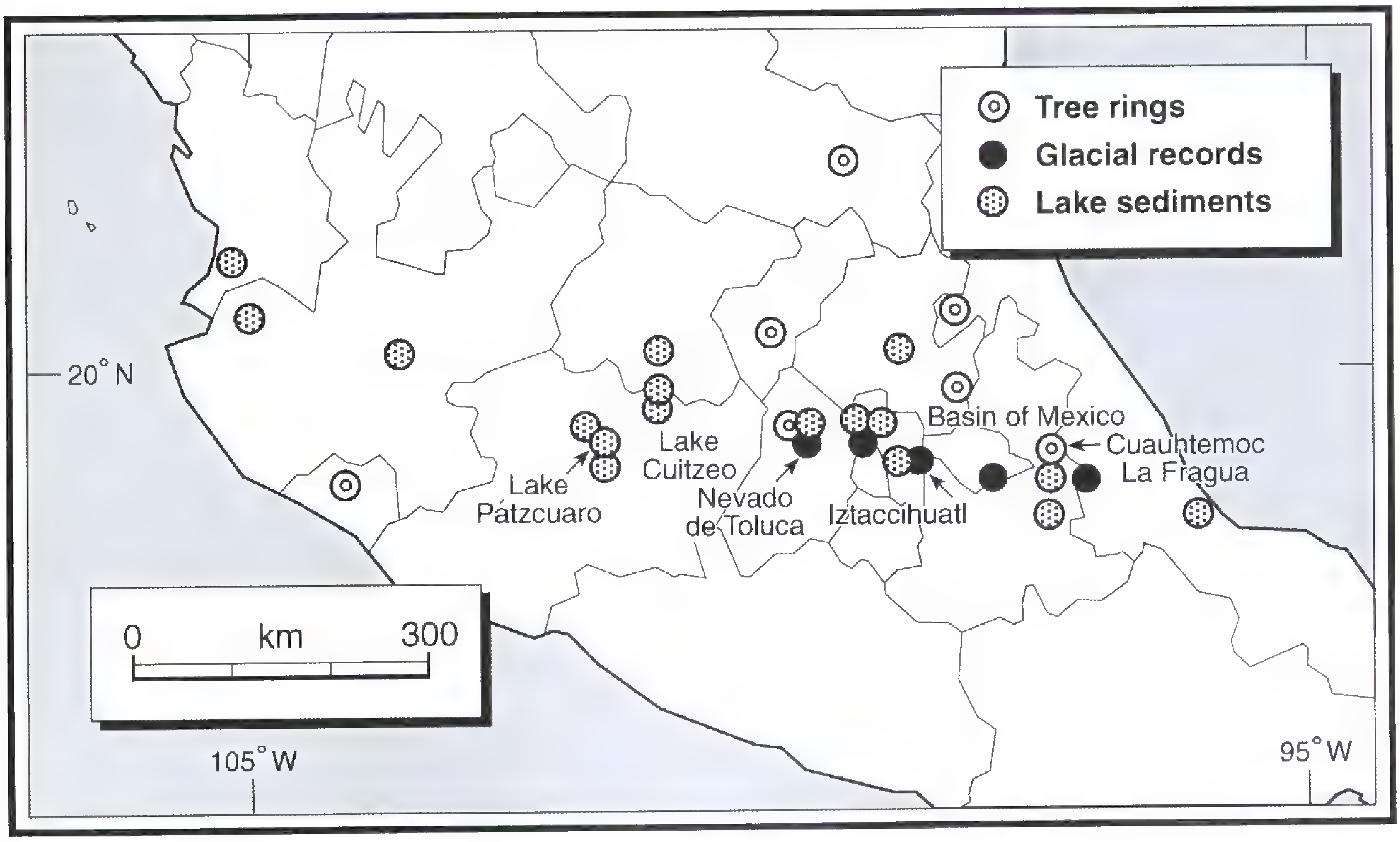

Figure 6. Sources of paleoclimatic data for the Trans-Mexican Volcanic Belt. Sites referred to in the text are named.

sheet (COHMAP Members, 1988; Thompson et al., 1993; Benson et al., 2003). There are signs of fluctuating conditions around the LGM. Conditions wetter than present persisted into the early Holocene, even as temperatures increased. Earlier debates about the source of early Holocene moisture remain largely unresolved, although it appears that summer rainfall became established earlier in the Chihuahuan Desert than in the Sonoran Desert. Greater effective moisture in the early to mid-Holocene is attributed to increased summer precipitation driven by insolation forcing. By about 5000 BP, conditions seem to have become drier, with fully modern environments being established from about 4000 BP. There is some evidence for wetter conditions around 3000 to 2000 BP.

Over the last 1000 years, tree rings provide very high-resolution paleoclimatic data, and the number of records is increasing rapidly. Most of the records from northern Mexico come from Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco), with the longest sequence coming from Durango (AD 1376 to 1993). The Durango record from Cerro Baraja and El Salto (Fig. 5) (Acuna-Soto et al., 2002; Cleaveland et al., 2003) shows the importance of winter precipitation for soil moisture and subsequent tree growth, even in an area where summer rainfall dominates. It shows that persistent/recurrent La Niña conditions, with dry winters, lead to drought (for the trees). The most severe droughts in the record occurred between 1540 and 1579 (the "Megadrought," which was also associated with epidemics of hemorrhagic fever), in the 1860s, and in the 1950s (this major drought also affected the southern and southwestern U.S.A.). Relating the tree ring records to instrumental climate records and historical data has shown that tree rings respond to ENSO and to the onset and strength of the summer monsoon (Diaz et al., 2002; Therrell et al., 2002). Unfortunately, none of the other proxy records cover this time period or have this resolution.

Trans-Mexican Volcanic Belt

This area is quite different from northern Mexico. It is geologically recent, is tectonically and volcanically active, and has long been a focus for human settlement. The tectonic disruption of a fluvial network has created a large number of lake basins, most of which still contain water (except where drained deliberately or affected by groundwater abstraction). As described above, a number of the highest peaks are still glaciated and a larger number were glaciated in the past. These offer an additional source of information (Fig. 6).

Lake sediments provide the greatest number of records from the TMVB (Fig. 6); these are mainly for the late Pleistocene and Holocene. To date, the records have been low resolution, partly because of sampling and dating, but also because there are few lakes that deposit laminated sediments. The interpretation of lake sediment records in terms of paleoclimate is affected by tephra deposition and the impact of long-term anthropogenic activity. Some pollen

records have been interpreted in largely anthropogenic terms (Goman & Byrne, 1998). Previously published records reveal very complex patterns of change (Metcalfe et al., 2000; Caballero et al., 2002). In the late Pleistocene, there may be a contrast between the western part of the region (wetter than present) and the eastern part (drier than present) (Bradbury, 1997). The terminal Pleistocene seems to have been very dry in many areas, with wetter conditions being established in the early Holocene. There are indications of dry conditions around 5000 BP followed by more overall variability in climate in the second half of the Holocene. Many records show evidence for human impact on the environment over the last 3500 years, but there is some evidence for another dry episode around 1000 BP.

As in northern Mexico, there are few long climate records, but a 27 m core from Lake Cuitzeo (Fig. 6) may extend back more than 120,000 years (Israde et al., 2002). The present lake is highly alkaline and saline and has a maximum depth of less than 2 m. The age of the base of the core is only an estimate because the oldest ^{14}C date, 42,400 BP, is from 9 m. There are a number of substantial volcanic deposits in the core, including a 70-cm thick ash layer dating to around 25,000 BP. The base of the sequence (ca. 120 to 90,000 BP, equivalent to MIS 5) indicates a freshwater lake of moderate depth, with a lake transgression being indicated at the end of the period prior to the deposition of 10 m of silts, clays, and volcanic deposits. The mid-Pleistocene saw a brief deepening, followed by shallowing and increasing salinity. Around 35,000 BP, the lake was very low. After deposition of the 70 cm of ash, the lake became deeper again (around the LGM), but then shallowed. Pollen data (Velazquez Duran et al., 2001) reflect conditions wetter than present between 35,000 and 22,000 BP, with pollen of alder (*Alnus* Miller), hornbeam (*Carpinus* L.), hazel (*Corylus* L.), and willow (*Salix* L.). Unfortunately, there is a hiatus between ca. 17,650 and 8000 BP. This may reflect a dry period similar to that recorded in the northern part of the Basin of Mexico (Caballero et al., 1999), but recent isotope data for part of this period from another core from Cuitzeo indicate wet conditions. Very low lake level, with a possible hiatus, is indicated around 5000 BP, and the lake has been shallow and increasingly saline over the last 3000 years. These conditions seem to have been particularly pronounced over the last 1000 years. The record from Cuitzeo shows strong similarities to that from Babicora (see above), although conditions for the key period from the LGM into the early Holocene remain unresolved.

Lake Pátzcuaro is one of the best studied basins in the TMVB. Watts and Bradbury (1982) and Bradbury (2000) provide details of a record from the southern part of the lake covering the last 44,000 years. This indicated wet conditions in the basin in the full glacial and latest Pleistocene. Drying apparently only set in from the mid-Holocene, although the record was confused by human impact. Cores from the north and southwest of the basin (Metcalfe et al., in prep.) confirm the persistence of a relatively deep lake in the basin through the LGM and into the early Holocene. As in Babicora, a change in the dominant diatom taxa at the start of the Holocene seems to indicate a change in the seasonality of precipitation from winter-dominated to summer-dominated. The later Holocene record shows increased inputs of soil from the catchment, but analysis of $\delta^{18}O$ on authigenic carbonates and the occurrence of multiple ostracod layers show a number of episodes of drying. One of these episodes occurred shortly after AD 1342 to 1396 (calibrated ^{14}C date), corresponding to evidence for low lake level from an archaeological site in the southwestern part of the basin (Fisher et al., 2003) and to early documentary evidence for drought from the Basin of Mexico. From this basin, it is clear that lake sediment records have the potential to record climatic change of the recent past, but they must be interpreted with care.

Some of the highest peaks of the TMVB preserve records of glacial advance, although whether the glaciers in central Mexico responded to temperature or precipitation (or some combination of both) is still not clear. Early work on the area's glacial history was carried out in the 1950s and 1960s (e.g., White, 1962), with further studies by Heine (1988). Unfortunately, there was disagreement over both the identification of moraines and the timing of events. More recent work has used cosmogenic exposure dating (in situ ^{36}Cl), K-Ar, and dated tephras to improve the chronology (e.g., Vázquez Selem, 1998). It now appears that the maximum extent of glaciation of Iztaccihuatl occurred between about 150,000 and 126,000 BP (Vázquez Selem & Heine, 2004). This coincides with the high stand at Lake Cuitzeo. There were also advances (on Iztaccihuatl and the Nevado de Toluca, Fig. 6) in the late Pleistocene (including the LGM), when the equilibrium line altitude was about 1000 m below present. The Nevado de Toluca records readvance in the Younger Dryas (when conditions seem to have been relatively dry) and in the late Holocene. Global evidence from tropical glaciers suggests that cold conditions alone are not sufficient for glacial expansion (L. Thompson, pers. comm.); they must have some source of moisture. Given the location of Mexico's highest mountains, however, it is possible that at different times they could have received moisture from either tropical or midlatitude sources.

In many parts of the world, pollen records have played a key part in reconstructing climate change (Hooghiemstra, 2006). Unfortunately, pollen records from the TMVB have been difficult to interpret and are not always consistent with other proxies (Lozano García & Xelhuantzi López, 1997). They are also strongly affected by human activity in catchments. A pollen record from a very high altitude site (3860 m) avoids human impact and provides evidence of tree line fluctuations since the late Pleistocene (Lozano García & Vázquez Selem, 2005), reflecting the interaction of precipitation and temperature. The record indicates that the tree line was 700 to 500 m below present in the late Pleistocene/early Holocene. The forest expanded in the early mid-Holocene (ca. 6500 to 6000 BP) under warmer and wetter conditions, but was then replaced by grassland as the climate dried through to about 5000 BP. Wetter conditions are indicated about 3000 BP (by the presence of *Pinus hartwegii* Lindley), corresponding to the period of wetter conditions in northern Mexico and ice readvance on some on the peaks of the TMVB. Cooler and moister conditions are also indicated around 2000 BP. The location of this site close to the boundary between forest and alpine grassland makes it climatically sensitive. A similar picture of lowered treeline and an expansion of alpine grassland in the late Pleistocene has also been recorded in the Upper Lerma basin (2570 m) (Lozano García et al., 2005). Sites at lower altitudes in the TMVB appear not to be as climatically sensitive and are more likely to be affected by human activity through the Holocene.

The late Holocene climatic variability indicated by lake and bog records is also confirmed by tree ring records emerging from this part of Mexico. The TMVB and states immediately to the north (e.g., San Luis Potosi) have recently become a focus for dendroclimatology. Records from this area seem to be most sensitive to summer precipitation (unlike those from Durango, see above). A climatic record from Douglas fir tree rings from Cuauhtemoc La Fragua, Puebla (Stahle et al., 2003), covering the period AD 1474 to 2001 has been correlated with maize (*Zea mays* L.) yields. Seven periods of low yield coincide with drought, famine, and social unrest. Tree ring records clearly have considerable potential, especially when combined with historical records (Therrell et al., 2004), to extend our knowledge of climate change back from the rather short-term instrumental records and forward from the more traditional geological archives. Even tree ring records, however, are not immune from human impact. A Montezuma bald cypress (*Taxodium mucronatum* Tenore) record from Chapultepec Park in the center of Mexico City (Villanueva-Diaz et al., 2003) appears to lose its climate/ring width relationship over the last 80 years as a result of effects of groundwater abstraction.

There is still little evidence from the TMVB for conditions in the last interglacial period, but there is some indication that it was wet. The mid-Pleistocene may also have been wetter than the late Pleistocene; this contrasts with the situation in northern Mexico. The pattern of conditions at the LGM still remains unclear because more records are needed from west of 101°W to confirm that it was indeed wetter, while the east was drier. Records from the Basin of Mexico indicate very dry conditions in the late glacial and early Holocene, but again there are few other records for comparison. Pátzcuaro was clearly not dry over this period. The patterns of change over the Holocene indicated by earlier studies have generally been confirmed with drier conditions around 5000 BP and again about 1000 to 900 BP.

Summary

Pleistocene conditions in Mexico were clearly very different from present conditions. Northern Mexico was much more forested (pinyon-juniper woodland, chaparral), with extensive lakes and wetland areas. In some areas, this woodland persisted for at least 30,000 years before the establishment of the modern desert scrub vegetation in the early to mid-Holocene (Van Devender, 1990b). The balance of evidence indicates that increased moisture was brought by westerly winds bringing more winter precipitation farther south than today. In central Mexico, glaciers and alpine grasslands expanded, and there were extensive forests of pine, oak, spruce, and alder. Evidence from farther south in Mexico, the Caribbean, and northern South America clearly indicates that the summer rainfall regime had largely broken down; therefore, it seems likely that some moisture reached this area from midlatitudes. Whether this was sufficient to drive higher lake levels in the west of Mexico and explains the expansion of glaciers on Mexico's highest peaks remains to be established. A transition toward the modern climate regime occurred about 9000 BP as the north of Mexico started to dry out. Pinyon-juniper woodlands retreated north, and spruce (*Picea*) died out. In the central highlands, very dry conditions are recorded in the Basin of Mexico, but there is little clear evidence from other sites. The early to mid-Holocene was warmer and wetter than present in both the TMVB and northern Mexico, presumably due to an enhanced summer monsoon in response to the insolation maximum. From about 4000 BP, modern desert conditions (desert scrub and succulents) became established in the north, and subtropical elements entered the TMVB (again, as

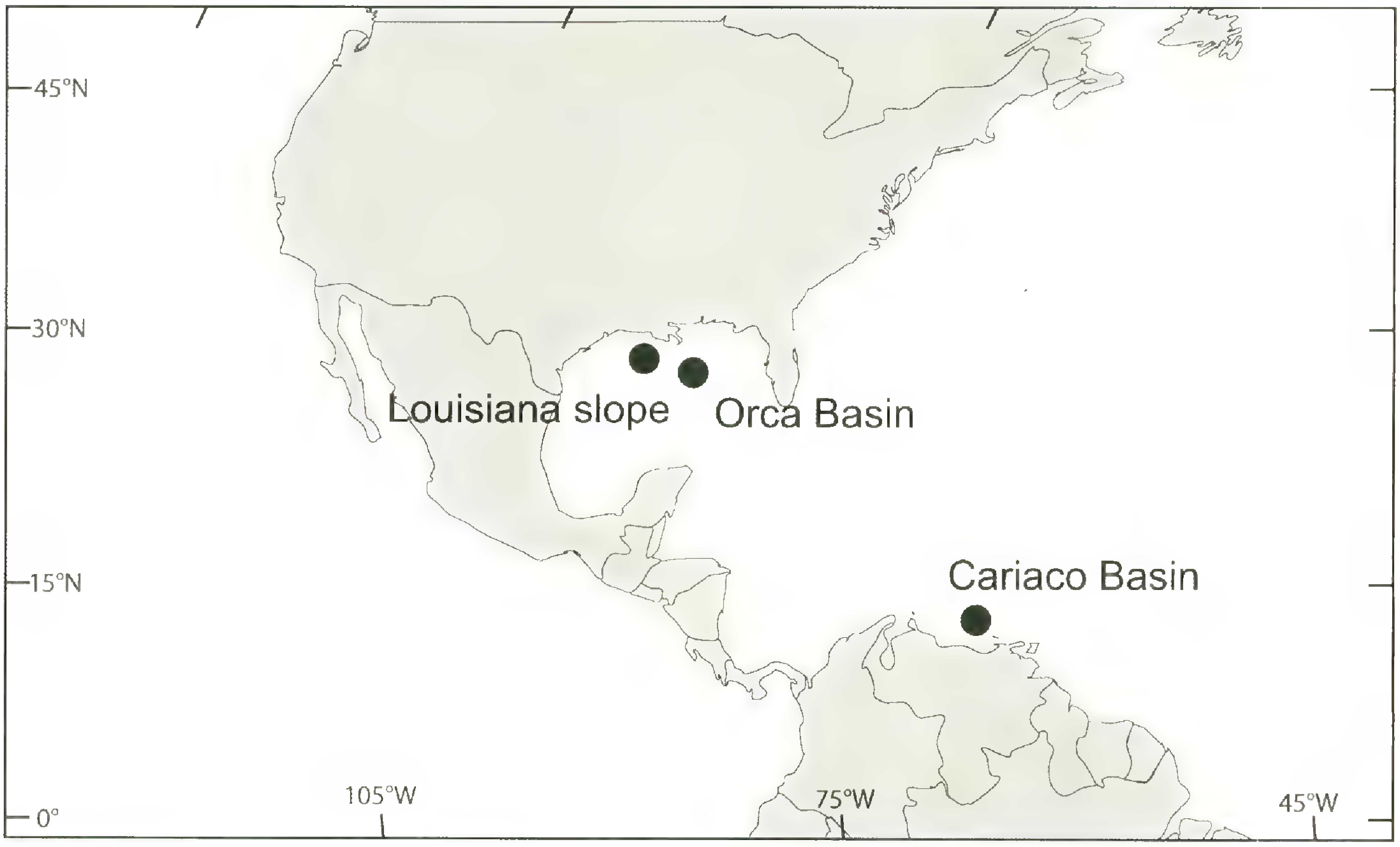

Figure 7. Locations of deep sea cores in the Gulf of Mexico and Caribbean basin referred to in the text.

present). Strong variability seems to mark the later Holocene, but many records from the north do not cover this period (no deposition or lack of preservation); furthermore, in the central highlands, records are confounded by human disturbance.

CAN WE IDENTIFY THE CAUSES OF CLIMATE CHANGE?

Changes in insolation (Milankovitch forcing), sea-surface temperature, the extent and height of the Laurentide ice sheet, and CO_2 concentrations have all been identified as possible drivers of climatic and vegetation change over the late Quaternary. There is also increasing interest in the timing and magnitude of ENSO, or ENSO-type, events and their impact on Holocene climate change. The inevitably patchy terrestrial records of change provide some indication of the role of these forcings. Evidence for the influence of insolation and the Laurentide ice sheet is clear from the literature, and CO_2 concentrations have played some role in vegetation change, at least regionally (Huang et al., 2001). Some further evidence can be derived from deep sea cores from the Gulf of Mexico/tropical Atlantic (Fig. 7). Results from the Orca basin and Louisiana slope (Broecker et al., 1989; Poore et al., 2003) have shown pulses of meltwater from the Laurentide ice sheet entering the Gulf of Mexico periodically from as early as 16,000 years ago. The occurrence of three major pulses in the late glacial period has been well established (Kennett et al., 1985), but Aharon's (2003) study shows renewed inputs of meltwater between about 9900 and 8900 years ago. These inputs may help to explain why the summer rainfall regime in the circum-Caribbean region did not become fully established until the early Holocene, lagging the insolation forcing. Hence, the influence of the Laurentide ice sheet has to be considered both through its rearrangement of upper air circulation and the impacts of its meltwater. While meltwater entering the Gulf of Mexico might seem the most likely to have affected the climate of Mexico, an increasing number of records (including those from the Gulf of California) indicate that meltwater pulses into the North Atlantic (Heinrich events) also had an effect on the Mexican climate.

Some of the most detailed ocean records have been obtained from the Cariaco Basin off the coast of Venezuela (Fig. 7), where upwelling results in laminated sediments. Haug et al. (2001) report evidence from the Cariaco Basin for shifts in the location of the ITCZ since the last glacial period. Concentrations of Ti in the sediments are used as a proxy for runoff from the adjacent land, which itself responds to the changing location of the ITCZ driven by insolation and ENSO. The long-term record shows runoff increasing in the early Holocene as the ITCZ moved north in response to insolation, but then decreasing from the mid-Holocene as the ITCZ returned southward. At this time, drying occurred in

the Caribbean, central and northern Mexico, and tropical north Africa. Dry events are recorded in the Younger Dryas and at 8200 BP in response to cooling in the North Atlantic. At higher resolution, the record shows the importance of the equatorial Pacific through the onset of stronger ENSOs from about 5000 BP (also seen in the Guymas Basin). The impact of ENSO is seen in the position of the ITCZ, which lies farther to the north in La Niña years and farther to the south in El Niño years. At the highest resolution, annual variations in insolation occur on time scales of the solar cycles (e.g., 11, 22 years). These solar cycles have also been detected in lake sediment records from the Yucatan peninsula (Hodell et al., 2001).

Conclusions

A number of important questions relating to the nature and timing of late Quaternary climatic change in northern and central Mexico remain unresolved. In some cases, it may simply be a matter of working on more sites to try to fill some of the gaps in our knowledge. Late glacial and early Holocene conditions were very strongly influenced by the Laurentide ice sheet and its history. Reorganizations of the major features of the atmospheric circulation in the late Pleistocene led to major changes in seasonality and amount of precipitation. These changes in precipitation were reflected by significant changes in vegetation distribution, bringing together assemblages of plants not found together today. Evidence for early warming seems to be recorded in some deep sea core records, but is not apparent in the terrestrial records. The modern summer rainfall regime only became fully established after 9000 BP, and the early Holocene was probably wetter over wide areas than today. Changes through the Holocene are consistent with insolation forcing, the resulting position of the ITCZ, and enhanced monsoon precipitation (Harrison et al., 2003; Ruter et al., 2004). So far, only deep sea core records show the onset of the modern ENSO regime from the mid-Holocene, although many different types of proxies show increased climatic variability after this time. Only the highest resolution records (annually laminated deep sea cores and tree rings) show ENSO and solar cycles.

It is clear that we still need better understanding of what drives change in many of the systems from which we derive our paleoclimatic records (e.g., vegetation, glaciers, lake levels). Better monitoring in the present day would help, but it does seem that there may be no analogues for conditions at certain periods in the past. The better integration of terrestrial and marine records should improve our understanding, but as the examples from the Gulf of California indicate, this is not always a straightforward task. Obtaining continuous, long, high-resolution terrestrial records would facilitate this comparison. For the more recent past, the integration of proxy records with historical and instrumental data could shed more light on both the nature of climatic variability and the ways in which human societies have coped (or not) with the vagaries of the climate system.

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QUATERNARY ENVIRONMENTAL HISTORY AND AGRICULTURAL IMPACT ON VEGETATION IN CENTRAL AMERICA

Dolores R. Piperno[1]

ABSTRACT

The corpus of historical data from lake sediments relating to the climate, vegetation, and human land use of the lowland Central American tropical forest between ca. 20,000 BP and the time of European contact is reviewed. Pollen, phytolith, and charcoal records identify the distribution and composition of tropical vegetation and fire patterns during the late Pleistocene, when they were significantly altered from today's, and earliest Holocene, when plant communities reassembled and interglacial representatives began to coalesce on the landscape. The significance of the environmental perturbations that occurred during the transition from the Pleistocene to the Holocene for human occupation of the lowland tropical forest and the geography and chronology of agricultural origins is discussed. Fire was employed by hunters and gatherers and farmers alike during the past 11,000 years as a primary tool of forest modification. The profound effects of an ancient pre-Columbian development of plant food production and, subsequently, slash and burn agriculture between ca. 10,000 BP and 1000 BP can be seen on lowland forests from Mexico to the Amazon Basin.

Key words: Climate, human land use, prehistoric agriculture, Quaternary history, seasonal tropical forests, slash and burn cultivation, vegetation.

RESUMEN

Se revisa la recopilación de datos históricos de sedimentos lacustres que conciernen el clima, la vegetación y la utilización humana del suelo de los bosques tropicales de tierras bajas de América Central entre ca. 20,000 A.P. y el momento de contacto europeo. Registros de polen, fitolitos y carbón identifican la distribución y composición de la vegetación y los patrones de fuego durante el Pleistoceno tardío, cuando fueron marcadamente alterados en relación al presente y al inicio del Holoceno, cuando las comunidades de plantas se reasociaron y los representantes interglaciales comenzaron a unirse en el paisaje. Se discute el significado que las perturbaciones ambientales durante la transición del Pleistoceno al Holoceno tuvieron en la ocupación humana del bosque tropical de tierras bajas, y la geografía y cronología de los orígenes agrícolas. El fuego fue empleado por cazadores y recolectores y granjeros por igual durante los últimos 11,000 años como una herramienta primaria de la modificación del bosque. Los efectos profundos de un antiguo desarrollo pre-colombino de la producción de plantas alimenticias y, posteriormente, de la agricultura de tala y quema entre ca. 10,000 AP y 1000 AP pueden verse en los bosques de tierras bajas desde México hasta la cuenca amazónica.

This paper presents a summary of Late Pleistocene and Holocene environmental conditions in the Central American lowland tropical forest. Natural and human-caused changes in vegetation and climate that occurred during the past 20,000 years are discussed with reference to the accumulated evidence acquired from botanical and minerological studies of lake sediment cores. Insights that historical data may provide about how to best conserve and restore tropical forests are also outlined. I focus primarily on paleoecological records that date to the Late Pleistocene and early Holocene periods. Debates surrounding vegetation and climate in the tropical forest during that time have been fervent and long-standing, but now appear to be converging on a consensus with regard to some important issues. I do not provide a systematic overview of the Holocene-aged records for climate change now available from lower elevations of Central America. The quality and quantity of information dating to the past 10,000 years are rapidly increasing, and it is beyond the scope of this paper to cover it (see Grimm et al., 2001, for an excellent review, including the burgeoning literature on the timing and effects of past ENSO (El Niño/Southern Oscillation) cycles). I do attempt to provide a more thorough examination of the evidence for past human influences on the lowland tropical forest—including a discussion of a few of the most important records from South America—from the initial stages of colonization, through the earliest periods of agriculture, until the arrival of Europeans. The reader should nonetheless bear in mind that it is possible to cite but a small fraction of the associated archaeological literature generated during the past 20 years.

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Paleoecological data attesting to the considerable changes in climate and vegetation that impacted the lowland Neotropical forest during ice ages have accumulated primarily during the past 25 to 30 years. Before that, because direct empirical information was very limited, theories of environmental stasis dominated questions concerning tropical forest ecology and environmental history, including explanations of species diversity (e.g., Fisher, 1960; Slobodkin & Sanders, 1969). These theories were elegant, and at the time they made a good deal of sense because it was logical to assume that the presence of a constantly warm and wet climate over millions of years would promote a continuous accumulation of species while creating little stress on the existing biota and causing only low rates of extinction.

At about the same time that theories of long-term tropical environmental stability held influence, what would become a famous archaeological debate was developing over the importance of ancient human occupations in the tropical forest. The dry highland regions of Mesoamerica and South America, where the (then) best understood and most famous high civilizations had arisen in the New World, were viewed by some prominent prehistorians as the major sources of most pre-Columbian cultural innovations and advances, including crop plant origins, pottery manufacture, and large and permanent village settlements (e.g., Mangelsdorf, 1953; Mangelsdorf et al., 1964; Meggers, 1954, 1971). Skepticism abounded in these circles as to whether the tropical forest was a fit environment for human habitation and innovation, including the development of effective agricultural systems (Mangelsdorf, 1953; Meggers, 1954, 1971; see Sauer, 1950, 1952, and Lathrap, 1970, 1973a, for the alternative viewpoint that tropical forest cultures *had* been very important). Some scholars would argue into the 1980s that the first people to colonize Central and South America largely avoided tropical forest, and that they and later tropical hunters and gatherers could not have survived for long without access to a cultivated food supply because wild food resources were scarce (e.g., Hart & Hart, 1986; Bailey et al., 1989; Sponsel, 1989).

Consequently, the degree to which cultural forest modification had taken place during the pre-Columbian era was in serious question. The "Ecologically Noble Savage" concept that tropical forest peoples lived in harmonic balance with their natural resources, minimally disrupting the landscapes on which they settled, was in full, politically-correct swing (see Alvard, 1993, and Dods, 2002, for a good discussion of the Noble Savage concept in anthropology and its historical antecedents). Descriptions of the extant tropical forest as "pristine" floral communities practically untouched by the human hand were common in both the anthropological and ecological literature.

During the 1960s and 1970s, pioneering studies by Van der Hammen and Gonzalez (1960), Livingstone (1975), and Martin (1964) provided the first empirical data demonstrating that highland regions occupying tropical latitudes in Africa and America experienced dramatic climatic and vegetational changes at the same time periods during which glaciations were strongest in higher latitudes of the Northern Hemisphere. These investigations, along with a now-classic application of environmental reconstruction through palynology in the Classic Maya area (Deevey et al., 1979), motivated similar research in the lowland tropics. Lakes with sediments rich in pollen and phytoliths that dated to the past 20,000 years, and thus that could provide evidence on the most extreme climatic oscillations of the last transglacial cycle, occurred more commonly in lowland tropical forest than was originally thought (e.g., Leyden, 1984, 1985; Bush & Colinvaux, 1988, 1990; Bush et al., 1989, 1992; Piperno et al., 1990). The furious constructions of modern reference collections of pollen and phytoliths that accompanied these initial paleolimnological efforts would lead to the identification of many of the lacustrine plant microfossils at more precise taxonomic levels than had been thought possible. It became clear that robust reconstructions of past environments through the same types of paleolimnology that had long been pursued in Europe and North America were achievable in the lowland tropical forest.

Also beginning in the 1970s and 1980s, archaeologists began to intensify their explorations in the tropical forest by investigating new areas and increasing their coverage of others. These efforts included carrying out intensive foot surveys using statistically significant sampling designs that not only identified more early human occupations, but also robustly documented regional trends in site number and size and population density through time (e.g., Cooke & Ranere, 1984; Lathrap et al., 1975). In addition, new and rigorous methods were applied to recover and study plant and other organic cultural remains (Pearsall, 1978; Piperno, 1985a, b, 1988). Traditional methods, such as the analysis of visible remains of seeds, fruits, and nuts, had not worked in studying early plant use and domestication and, indeed, were providing highly biased pictures of human plant exploitation because organic materials do not survive for long under the inimical warm and humid conditions found in the tropics. Our understanding of the natural and human processes affecting the lowland Neotropical forest during the

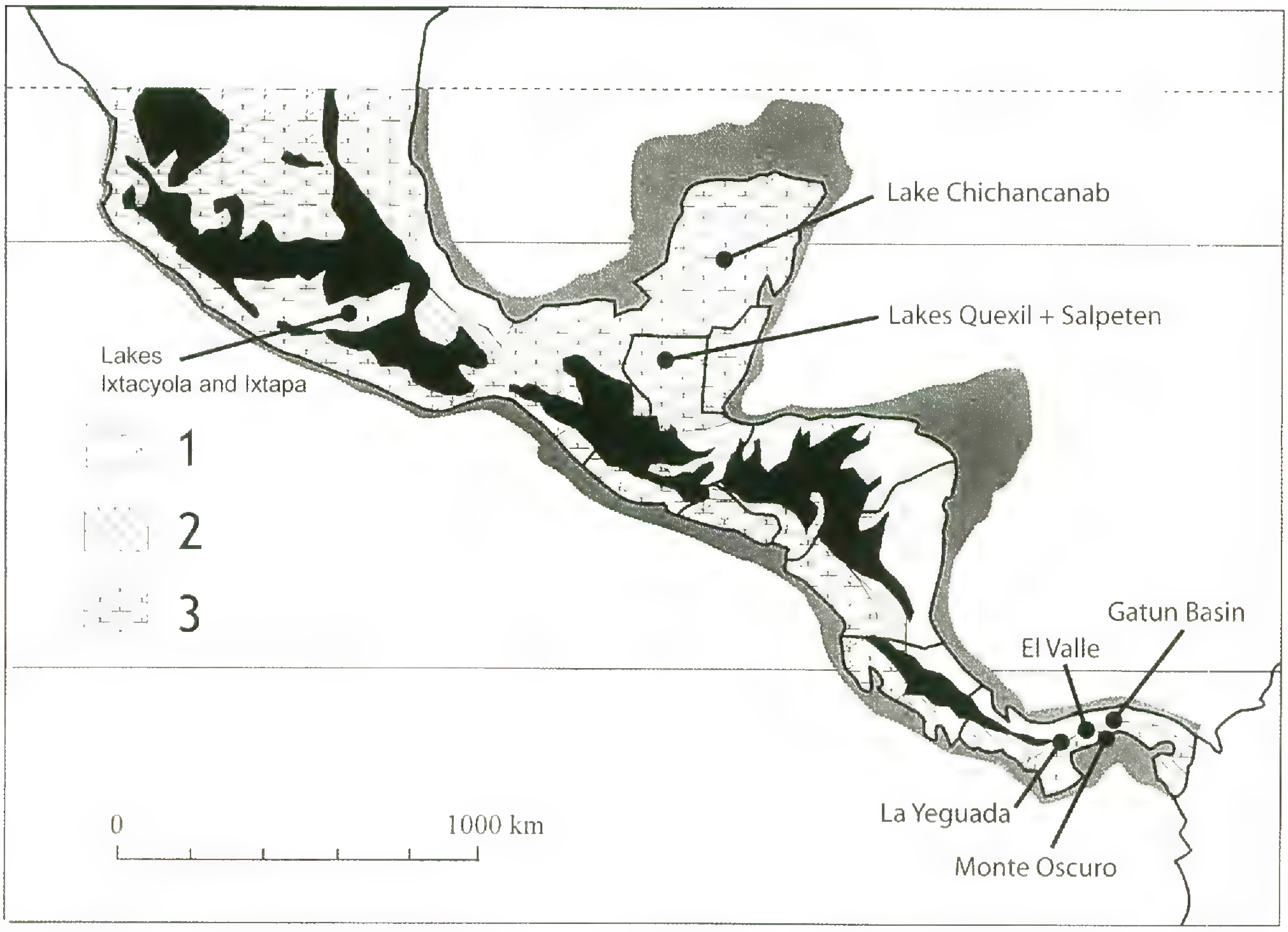

Figure 1. Location of paleoecological sites with records dating to the Pleistocene and the reconstructed vegetation of lowland tropical Middle and Central America between 20,000 BP and ca. 10,500 BP Gray areas represent land exposed by lowered Pleistocene sea levels at 18,000 BP, the period of maximum glacial advance. Black areas indicate elevations above 1500 m asl. Modified from Piperno and Pearsall, 1998: fig. 2.4, with permission from Elsevier. Sites and their investigators are as follows: Lake Chichancanab (Hodell et al., 1991); Lake Quexil (Leyden et al., 1993); Lake Salpeten (Leyden, 1987); La Yeguada (Piperno et al., 1990, 1991a; Bush et al., 1992); El Valle (Bush & Colinvaux, 1990; Piperno et al., 1991a); Gatun Basin (Bartlett & Barghoorn, 1973; Piperno et al., 1992); Monte Oscuro (Piperno & Jones, 2003); Lakes Ixtacyola and Ixtapa (Piperno, this paper, and Piperno et al., 2004). The vegetational reconstruction is as follows: (1) Largely unbroken moist forest, often with a mixture of presently high-elevation and lowland forest elements. In some areas, montane forest elements (e.g., *Podocarpus* L'Hér. ex Pers., *Quercus*, *Alnus* Mill., *Ilex*) were conspicuous. Annual precipitation was lower than today, but sufficient precipitation existed to support a forest. (2) Forest containing drier elements than characteristic today. High-elevation forest elements occurred, especially in moister areas of the zone. Areas near the 2000 mm precipitation isohyet and areas with sandy soils may have contained savanna woodland. The vegetation may have been patchy. (3) Mostly undifferentiated thorn woodland, low scrub, and wooded savanna vegetation. Some regions (e.g., Guatemala) had temperate elements (e.g., *Juniperus*). Areas receiving greater than 2000 mm of rainfall today may still have supported a drier forest, as in (2). River- and stream-side locations supported a forest.

past 20,000 years and more has been dramatically altered as a result of the above-mentioned work.

Late Pleistocene Vegetation and Climate

Most existing lake records of Late Pleistocene age from the Americas, including the tropics, date to not more than 20,000 to 25,000 years ago (all ages in the paper are in uncalibrated radiocarbon years). The bulk of the available data are, however, of an age appropriate for evaluating the problems addressed here because the final 10,000 years of the last transglacial cycle (between about 20,000 and 10,000 BP (before present)) has long been a period of intense interest to paleoecologists and archaeologists alike. It covers the Last Glacial Maximum (18,000 BP) and subsequent termination of the Pleistocene, and accommodates all now-accepted chronologies for human colonization of the Americas (Dillehay, 1997, 2000; Meltzer, 1997; Meltzer et al., 1994). Furthermore, although paleoecological records from the now-humid lowlands are still few in number, they originate from a representative spectrum of the major ecological zones found in the lowland Neotropics from ever-wet, aseasonal habitats to those characterized by a marked seasonality of rainfall.

Figure 1 shows the locations of the major lakes and large swamps in Central America that have yielded records dating to the Pleistocene period. Vegetational and other reconstructions derived from these paleoenvironmental sequences were often based on pollen, phytolith, diatom, and minerological data analyzed in

tandem. Figure 1 also contains a postulated reconstruction of vegetation for the Central America lowlands during the late-glacial period. For areas where sequences of Pleistocene age do not yet exist, I assumed the paleovegetation to be similar to the paleovegetation in areas which are presently similar ecologically.

The major environmental trends and patterns indicated from the records have been described in detail elsewhere (e.g., Bush et al., 1992; Leyden et al., 1993; Piperno & Pearsall, 1998) and are summarized herein. The lowland Neotropics between 20,000 and 10,000 BP appear to have been considerably cooler and drier than they are today. Reconstructions of tree line descent indicate that temperatures over land surfaces were from 4°C to 7°C lower than at the present time; these estimates are largely concordant with those derived from newer studies of Pleistocene sea surface temperatures derived from coral oxygen isotopes (Bush et al., 1992; Colinvaux et al., 1996; Guilderson et al., 1994; Leyden et al., 1993; Peltier & Solheim, 2004). The degree to which the Pleistocene precipitation was reduced is under considerable discussion. Many of the lakes shown in Figure 1 were lower or completely dry during the Late Pleistocene and, as will be described shortly, many of their watersheds appear to have contained few trees. These factors have led many investigators, the author included, to believe that intertropical annual rainfall was probably reduced on the order of about 30% to 50% (Leyden, 1984; Leyden et al., 1993; Piperno & Jones, 2003; Van der Hammen & Hooghiemstra, 2000). Others would disagree, believing that rainfall reduction was instead only about 10% to 15% below today's values (e.g., Colinvaux et al., 1996, 2000).

There is no doubt that glacial-age atmospheres contained much less CO_2 than they would after the Pleistocene ended (Barnola et al., 1987; Cowling & Sikes, 1999). CO_2 concentrations were 33% lower than preindustrial values (PIV) until ca. 12,500 BP, when they were still 25% lower than the PIV, not rising close to PIV values until about 9000 BP (Barnola et al., 1987). The lower CO_2 concentrations probably exerted significant influences on the vegetation in ways we do not understand very well at present (Cowling & Sikes, 1999; Mayle & Beerling, 2004). One possible major effect was that Pleistocene forest canopies were more open than today's due to lower light use efficiency during photosynthesis (Sage, 1995).

In many regions of the tropics these identified ice age conditions—much cooler, probably substantially drier, and with much lower atmospheric CO_2—persisted until 12,000 to shortly after 10,500 years ago, such that modern vegetation communities did not begin coalescing until that time. For example, at Lake Quexil, located in the Peten, Guatemala, seminal work by Barbara Leyden and her colleagues (Leyden, 1984; Leyden et al., 1993) showed that trees now characteristic of the modern semi-evergreen forest in the region are not recorded in pollen records until a short time after ca. 10,300 BP, and that it took at least another several hundred years before a well-developed tropical forest was established. During the Late Pleistocene, in contrast, the region was a cool and very dry place in which few trees grew.

Existing paleoecological data allow us to identify the following major, Late Pleistocene vegetational patterns. First, where the modern potential vegetation is deciduous or drier forms of semi-evergreen forest, a replacement of forest is evidenced by open vegetation similar to but probably not exactly equivalent with today's thorn woodlands, thorn scrublands, and savanna. This is empirically demonstrated in the lowlands of southwest Mexico, Guatemala, Haiti, and Pacific-side Panama, at Lakes Ixtacyola, Ixtapa, Quexil, Salpeten, and Monte Oscuro. Second, where today the annual rainfall is between about 2.6 and 4 m and the actual or potential vegetation is evergreen and semi-evergreen forest, the Pleistocene vegetation was largely forested. This is empirically demonstrated in Caribbean-side Panama at the Gatun Basin, as well as at Pacific watershed sites in Panama at elevations of between 500 and 700 m above sea level (asl), such as La Yeguada and El Valle. This situation presumably prevailed throughout the Caribbean watershed of Central Panama and other low lying wetter areas as well. At the middle elevation sites (ca. 500–1000 m asl) where the Pleistocene vegetation was forest (e.g., El Valle, La Yeguada), it can be seen particularly well how the arboreal component of the vegetation responded to the cooler temperatures; trees that today generally grow only in mountainous areas above 1500 m were forced about 800 to 1200 m downslope and co-existed with those lowland arboreal elements that were better at tolerating lower temperatures.

It is not surprising in view of all of this that few to none of the vegetational signatures from the Pleistocene appear to have modern analogues. There were different forest facies likely involving the reduction and partial replacement of lowland evergreen forest by arboreal elements now primarily confined to drier types of forest. However, because species-specific tree identifications usually cannot be made from pollen and phytolith records, details of forest composition are difficult to reconstruct with any certainty. This is an area of research where increasing our efforts to retrieve and identify seeds and other macro-fossil plant remains from lake sediments may prove to be rewarding.

Figure 2. The crater and surrounding rim of Monte Oscuro, Panama.

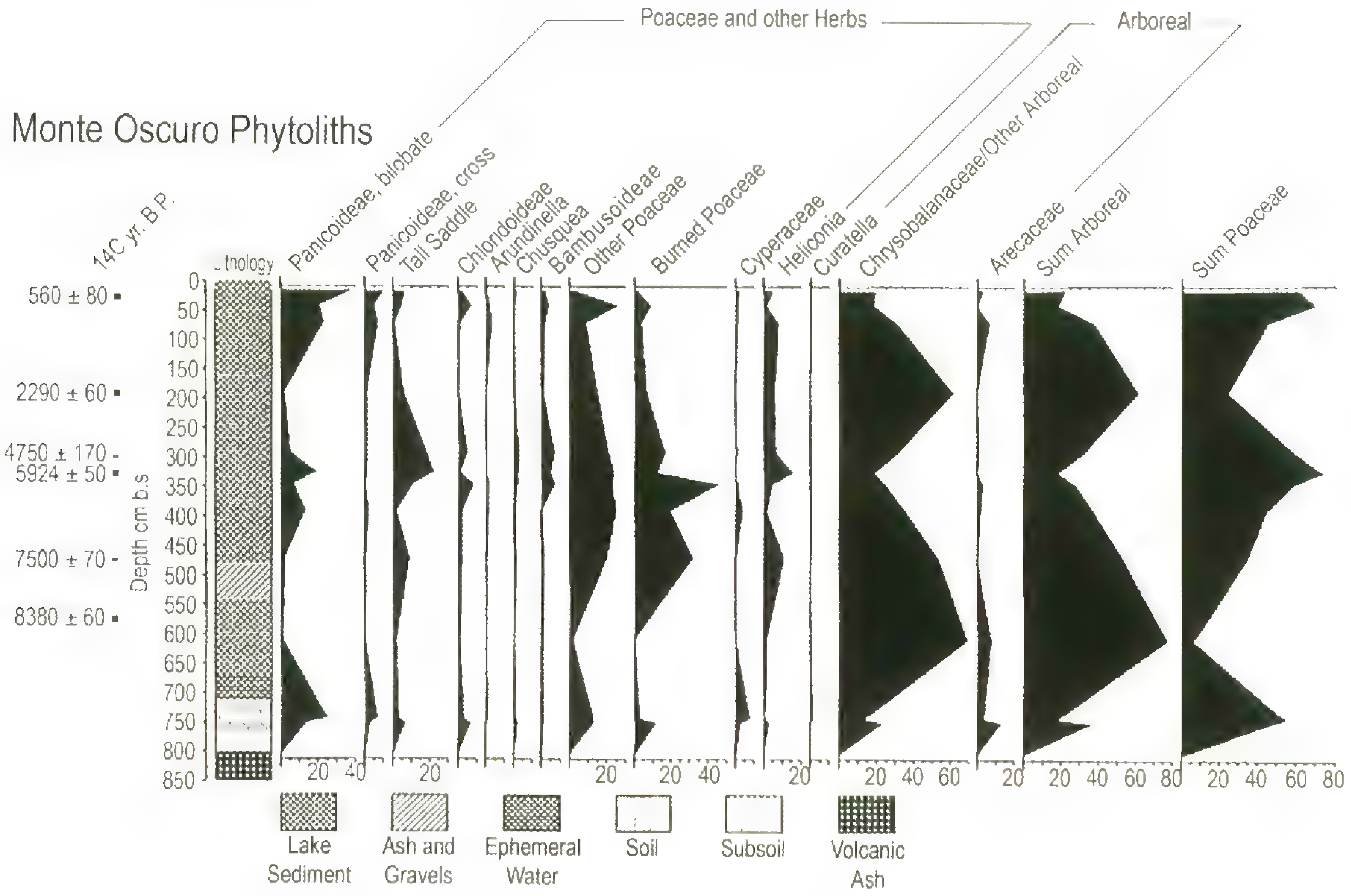

Figure 3. The percentage of each major phytolith taxon found at Monte Oscuro, Panama. The Chrysobalanaceae/Other Arboreal category contains predominantly Chrysobalanceae phytoliths (usually > 85%–90%), with contributions also from *Protium*, other Burseraceae, the Moraceae, Euphorbiaceae, Annonaceae, Connaraceae, and Flacourtiaceae. Percentages for burned Poaceae phytoliths were calculated separately. Only short cell phytoliths from grasses (e.g., bilobates, saddle-shapes) were studied for evidence of burning. Taxa attributions are as follows: *Chusquea* Kunth. (Poaceae). Reprinted from Piperno and Jones (2003), with permission from Elsevier.

The paleobotanical records from a few of these sites are now discussed in more detail to better illustrate the interpreted findings. The author and John Jones recently studied phytolith and pollen records from Monte Oscuro, Panama, a large lake located in an extinct crater 75 km west of Panama City where annual rainfall presently is 1.8 m (Piperno & Jones, 2003; Figs. 2–4). This sequence is the first from Panama dating to the Pleistocene from the seasonally dry Pacific coastal plain, where the potential vegetation is a deciduous tropical forest and the forests, therefore, would be particularly prone to

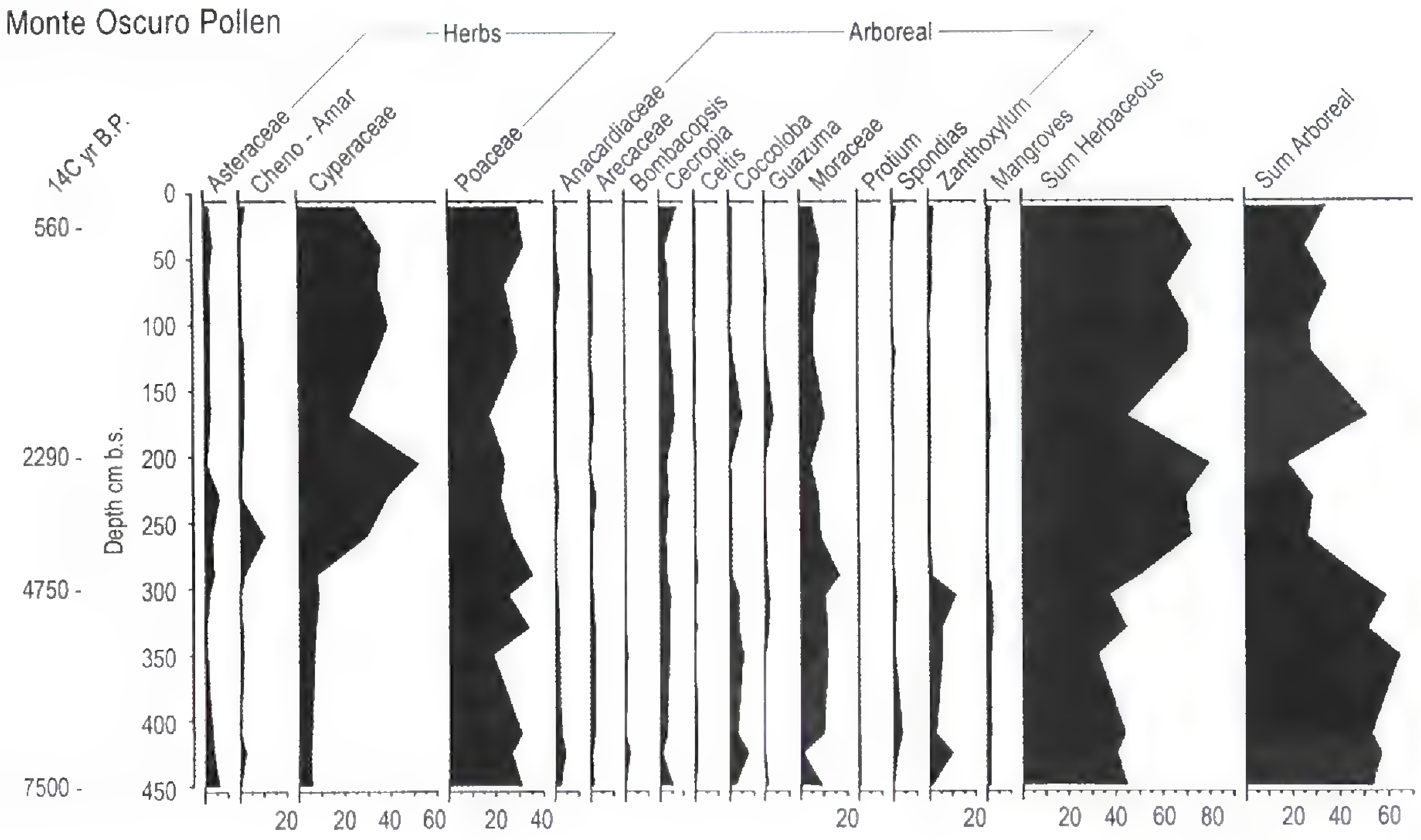

Figure 4. The percentage of each major pollen taxon found at Monte Oscuro, Panama. Cheno-Amar refers to Chenopodiaceae–Amaranthaceae. Taxa attributions are as follows: *Bombacopsis* (Bombacaceae) Pittier. Reprinted from Piperno and Jones (2003), with permission from Elsevier.

fragmentation under conditions of significant climatic drying. The sedimentary sequence from Monte Oscuro shows that during the Late Pleistocene the lake bed was persistently dry, such that a paleosol formed and supported an associated vegetation. Pollen is not preserved in these sediments because they were subjected to oxidation, but phytoliths are common.

The phytolith data from the paleosol indicate that during the Late Pleistocene, the Monte Oscuro region supported a vegetation containing many grasses, sedges, and other herbaceous plants (Fig. 3). The archetypal indicator of savanna in the Neotropics, the shrub or small tree *Curatella americana* L., is also present during this period. Trees that are characteristic of the modern deciduous forests of the area appear to have grown in low numbers. Grass phytolith morphology indicates that the Chloridoid (short grasses) and Panicoid (tall grasses) sub-families are common in the phytolith assemblages. These grasses predominantly use the C_4 photosynthetic pathway (only a small proportion of modern Panicoid grasses are C_3), further adding to the picture of a dry and open landscape. Charcoal (not shown) and burned grass phytoliths (Fig. 3) also occur, indicating that the landscape was periodically subjected to fires. During this interval, arboreal phytolith taxa are represented mainly by the Chrysobalanaceae and Arecaceae. There are a few phytoliths from *Protium* Basm. f., the Annonaceae, and the Moraceae, indicating these trees were also growing nearby.

At an estimated date of ca. 10,500 BP (at a depth of 7m), a substantial water table rise and initial ponding occurred, leading to the establishment of a permanent water body that lasted into the modern era. The date for the filling of the Monte Oscuro crater is consistent with the inundation of other lake beds in tropical America that were dry or much lower during the Late Pleistocene (Curtis et al., 1999; Ledru et al., 1998). Both the phytolith (Fig. 3) and pollen (Fig. 4) records show that during the early Holocene a diverse tropical deciduous forest expanded into the Monte Oscuro watershed. By 8300 BP, percentages of grass and sedge phytoliths had declined greatly from their Pleistocene occurrence frequencies and *Curatella* L. is no longer recorded at all. By shortly after 7500 BP, when sediments first contain high amounts of pollen, a number of trees occur in the pollen assemblages whose modern ecological affinity is seasonal tropical forest (e.g., *Zanthoxylum* L., *Spondias* L., *Protium*, *Bursera* Jack., *Erythrina* L., *Celtis* L., species of Anacardiaceae and Moraceae; other arboreal taxa such as *Trema* L., *Machaerium*-type, *Cavanillesia* Ruiz & Pav., and *Calophyllum*, which are not shown) (Fig. 4).

During the Pleistocene, the Monte Oscuro region supported open kinds of vegetation consisting of a large number and variety of herbaceous taxa, including grasses and sedges, and small shrubs and trees, including *Curatella* and palms, adapted to dry-land habitats. Trees that form important components of seasonal tropical forests in the region today were not entirely eliminated from the landscape but appear to have grown in low numbers. Some of them were probably growing along the margins of water courses. In light of these factors and the amount of modern annual precipitation the area receives, 1800 mm, it is

likely that annual rainfall in the Monte Oscuro region was reduced during the Late Pleistocene by at least 35%. It is also reasonable to extrapolate from the Monte Oscuro record to predict that a significant part of the Pacific coastal plain of the Panamanian land bridge was a dry and open habitat. It might be unwise, however, to use the word savanna to describe the Late Pleistocene vegetation. Thorny scrub associations (those with many legumes, cacti, and also some euphorbs) produce few phytoliths that can be identified even to the family level, and are thus difficult to document in phytolith records. It is likely that these types of plants were present on the landscape, perhaps in considerable number, and, along with the plant taxa that can be documented through their microfossils, formed species combinations that were well adapted to Pleistocene dry climatic phases but that do not at the present time grow together.

How heterogeneous and probably patchy the Pleistocene vegetation was across small distance scales in regions such as Panama, where one can move from tropical deciduous to tropical evergreen forest in a leisurely 90 minute car ride, is illustrated by the pollen and phytolith sequences from La Yeguada and El Valle studied by Mark Bush, Paul Colinvaux, and the author (Figs. 5, 6). These sites are located in the Pacific watershed uplands between 500 and 650 m asl (Fig. 1). They receive between 3 and 4 m of rainfall annually today, twice the amount as on the Pacific coastal plain where Monte Oscuro is located. The climate is still highly seasonal at these two sites: over 90% of the rain falls during the wet season and there is a long and marked dry season of five months' duration. In each case, the Pleistocene vegetation was a forest containing trees now found mainly at elevations of 1500 m and above, such as *Quercus* L., *Ilex* L., and *Magnolia* L. (Fig. 5). However, presence of the clay type illite—a mineral that typically forms when the soils and rocks of a lake's catchment are little weathered from rainfall—in the Pleistocene but not in the Holocene deposits at Lake La Yeguada (described in Bush et al., 1992) is a good indication that during the Late Pleistocene the region's precipitation was considerably less than today's. At El Valle, a surge in *Chenopodium* L. and *Alternanthera* Forssk. pollen between 19,000 and 12,000 BP indicates the lake contracted severely at that time, almost certainly a response to climatic drying (Fig. 6; Bush & Colinvaux, 1990).

The most recently generated data dating to the Pleistocene from the Central American lowlands, which are still in a preliminary state and cannot be discussed in detail here, come from the Central Balsas River Valley located in tropical southwestern Mexico, where no information on the paleoenvironment was previously available. The author began a project there five years ago to reconstruct the environmental and cultural history of the region. This is where the extensive molecular work carried out by John Doebley and colleagues during the past 15 years places the origin of maize, whose ancestor they have determined to be a species of teosinte, *Zea mays* L. subsp. *parviglumis* Iltis & Doebley, native to the Central Balsas region (e.g., Doebley, 1990; Matsuoka et al., 2002; Fig. 7). As over much of the Pacific watershed of Central America, the potential vegetation of the region is a tropical deciduous forest. Preliminary information from two lakes, Ixtacyola and Ixtapa, located in and near the Iguala Valley on the eastern side of the Central Balsas region at an elevation of 700 m asl (Fig. 1) suggests that there, also, the Late Pleistocene climate was much cooler and drier than today's and the glacial vegetation contained fewer trees than did early Holocene associations (Piperno et al., 2004).

Summary: What Have We Learned about Pleistocene Environments?

The Pleistocene climate in the lowland Neotropics is now understood to have been a peculiar combination of low temperature, precipitation, and atmospheric CO_2. The cumulative effect of these conditions on tropical plant communities and whether all were effecting community structure and floristic composition to an equally significant degree, are under considerable discussion. It has been suggested that low CO_2 concentrations alone might explain much of the displacement of forest by herbaceous vegetation seen in the Pleistocene lake records from Central and South America (e.g., Colinvaux et al., 2000; Mayle & Beerling, 2004). In order to more closely study this issue, Huang et al. (2001) analyzed leaf wax carbon isotopes in lakes from Chihuahua, Mexico (Lake Babicora), and Peten, Guatemala (Lake Quexil). It is well understood that the Chihuahua and Guatemala regions were, respectively, fairly wet and very dry during the Late Pleistocene due to being under the influence of different sources of moisture. Today, the two regions still experience contrasting precipitation patterns, which are the opposite of what they were during late glacial times. Huang et al. (2001) were able to show conclusively that at Lake Babicora there was much more C_3 vegetation during the late-glacial period than during the Holocene. The opposite was true at Lake Quexil, where, in accordance with the palynological data indicating the presence of open, dry-land environments, the Late Pleistocene vegetation was shown to contain many more C_4 plants than did the Holocene vegetation. The wet climate that

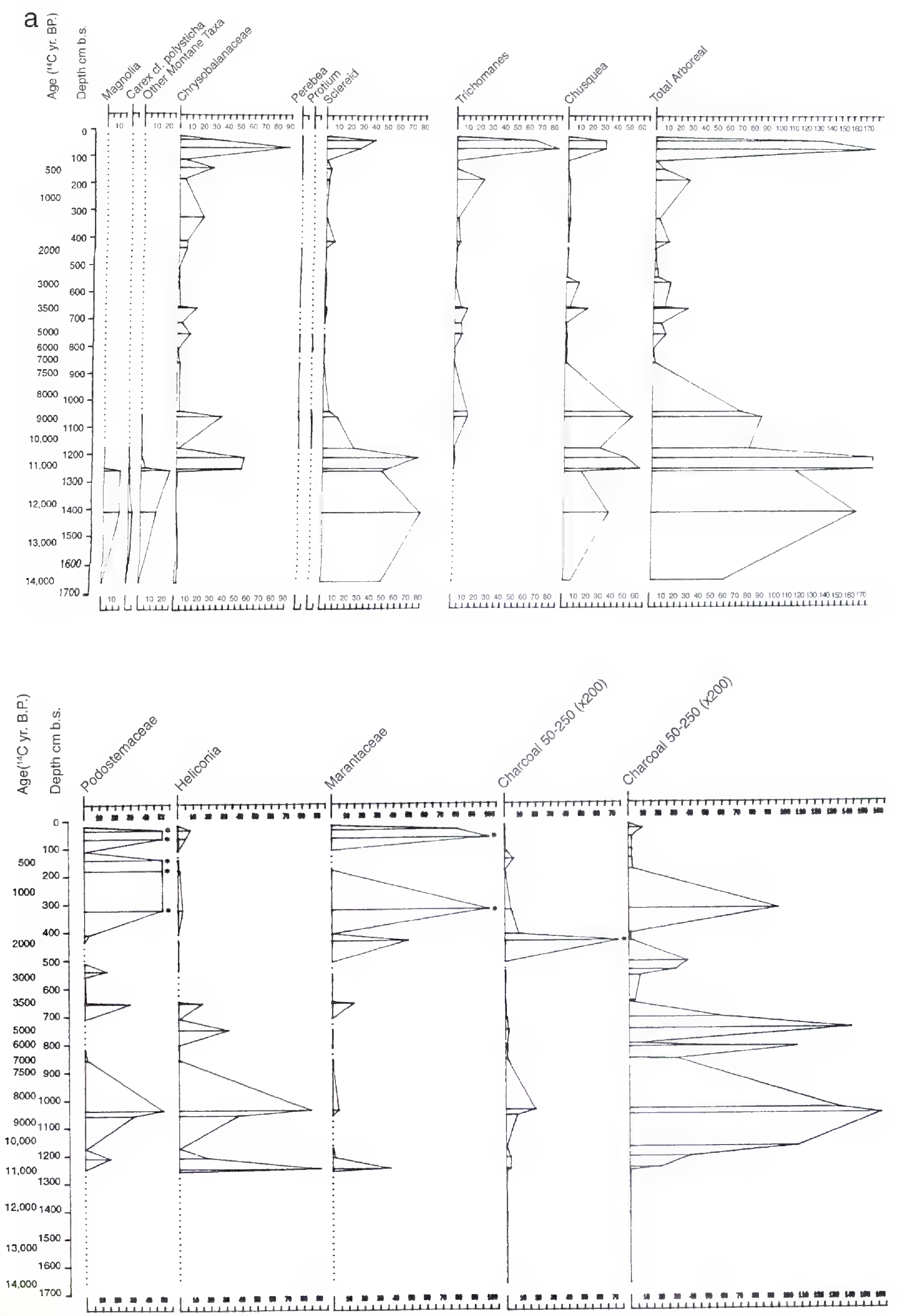

Figure 5a. A phytolith influx (number of phytoliths per 20 cm^2 per yr.) diagram from Lake La Yeguada, Panama. Taxa attributions are as follows: *Magnolia* L. (Magnoliaceae), *Carex* sp. ined. aff. *polysticha* Boeck (Cyperaceae), *Perebea* Aubl. (Moraceae), *Protium* Basm. f. (Burseraceae), *Trichomanes* L. (Hymenophyllaceae). From Piperno et al. (1991b).

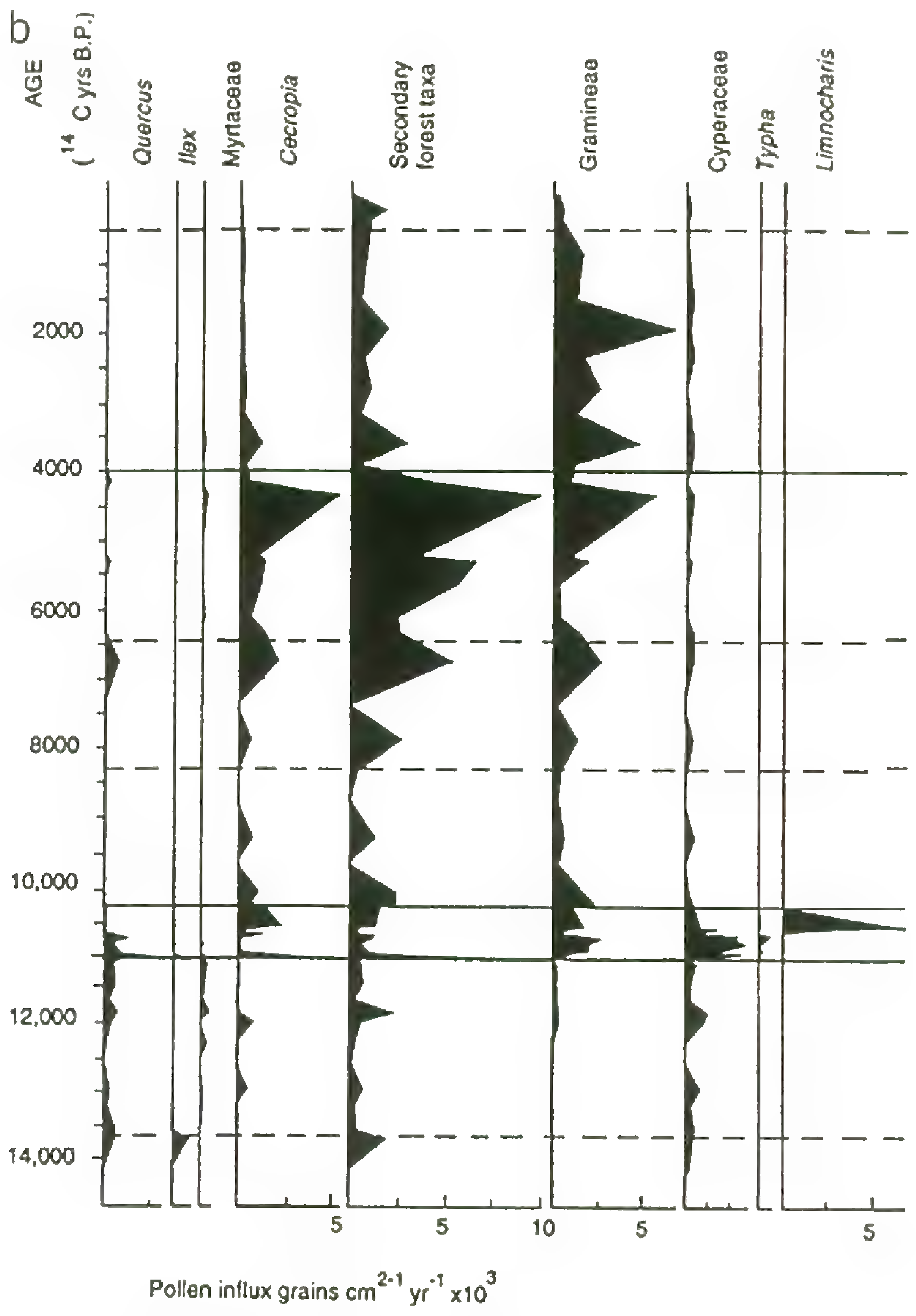

Figure 5b. A pollen influx (number of pollen grains per cm^2 per yr. $\times 10^3$) diagram from La Yeguada, Panama. Taxa attributions as follows: *Typha* L. (Typhaceae), *Limnocharis* Bonpl. (Butomaceae). From Piperno et al. (1991b).

prevailed at Lake Babicora thus had far more influence on the regional vegetation than the low atmospheric CO_2 concentrations did.

Therefore, vegetational shifts from C_3-dominated forests to C_4-dominated grasslands in the tropics cannot be driven without concurrent significant reductions in precipitation. Furthermore, low CO_2 concentrations acting largely separately from climatic influences probably cannot explain why many presently deep lakes from Mexico to southern Brazil were dry lake beds or shallow water bodies during the Late Pleistocene (e.g., Ledru et al., 1998; Leyden, 1984; Leyden et al., 1993; Piperno & Jones, 2003; Piperno et al., 2004) and why incontrovertible signals of substantially reduced precipitation, such as the evaporitic mineral gypsum and the clay illite, formed in some of them (Bush et al., 1992; Leyden et al., 1993). While low CO_2 may certainly have exacerbated drought stress and further promoted the expansion of C_4 and CAM open-land plants at the expense of some C_3 forest species, the tropical ice age climate appears to have been substantially cooler and drier.

Formerly thought to be incompatible physical forces of the Pleistocene climate, cooling and drying can now be understood to have been mechanistically and causally linked. The negligible amount of evaporation that took place over cooler tropical ocean surfaces, for example, meant that much less water vapor was available to become rainfall over adjacent land surfaces (Webb et al., 1997). The persistence of forest in higher precipitation areas such as at La Yeguada and El Valle, even under what the author and others think was probably a 30% to 40% decline of precipitation, is not surprising because sufficient moisture would still have been available to support species-diverse forests. Furthermore, in these C_3-dominated forests, cooler Pleistocene temperatures probably would have counter-balanced the effects of lower precipitation by improving carbon and water balance and reducing evapotranspiration gradients

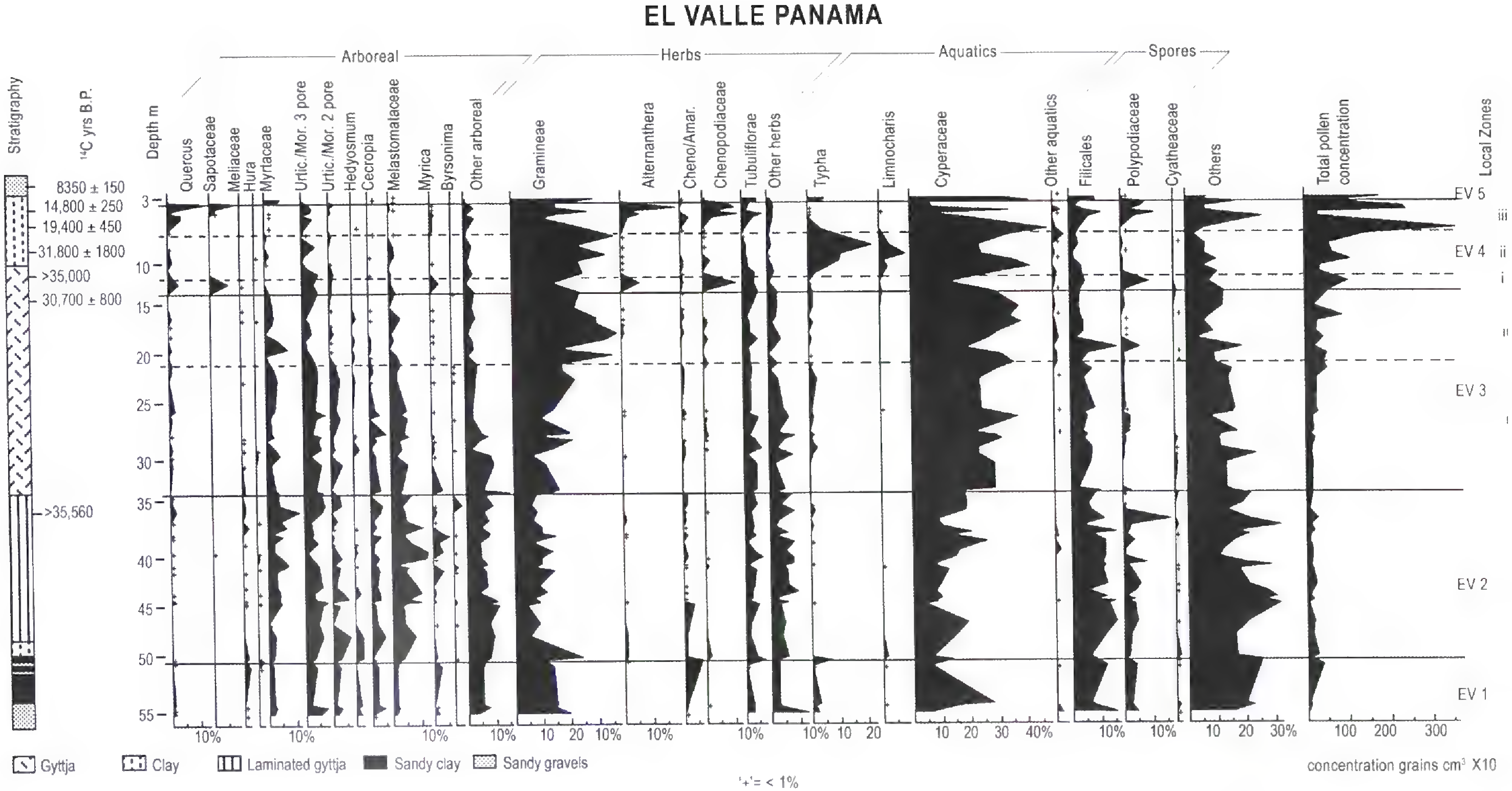

Figure 6. The percentage of each major pollen taxon found at El Valle, Panama. Total pollen concentrations are shown at the right. Taxa attributions are as follows: *Hura* L. (Euphorbiaceae), *Myrica* L. (Myricaceae), *Byrsonima* Rich. ex Kunth (Malpighiaceae), *Alternanthera* Forssk. (Amaranthaceae). Reproduced with permission from Bush and Colinvaux (1990).

Figure 7. The wild ancestor of maize, *Zea mays* subsp. *parviglumis*, growing in the Central Balsas River Valley, Mexico.

and photorespiratory carbon loss (Cowling & Sykes, 1999). In contrast to forest persistence in high rainfall zones, forests were often displaced by savanna/thorny scrub kinds of vegetation during the Pleistocene, where the modern potential vegetation is a highly seasonal forest with annual rainfall of 1.2–2 m a year. Here, the dry climate, aided by the effects of low CO_2, resulted in landscapes where forest growth was minimal.

The Central and South American lowland tropical forests are thought to house more plant species than the tropics of Asia and Africa combined (Richardson et al., 2001). There are increasing indications that a good deal

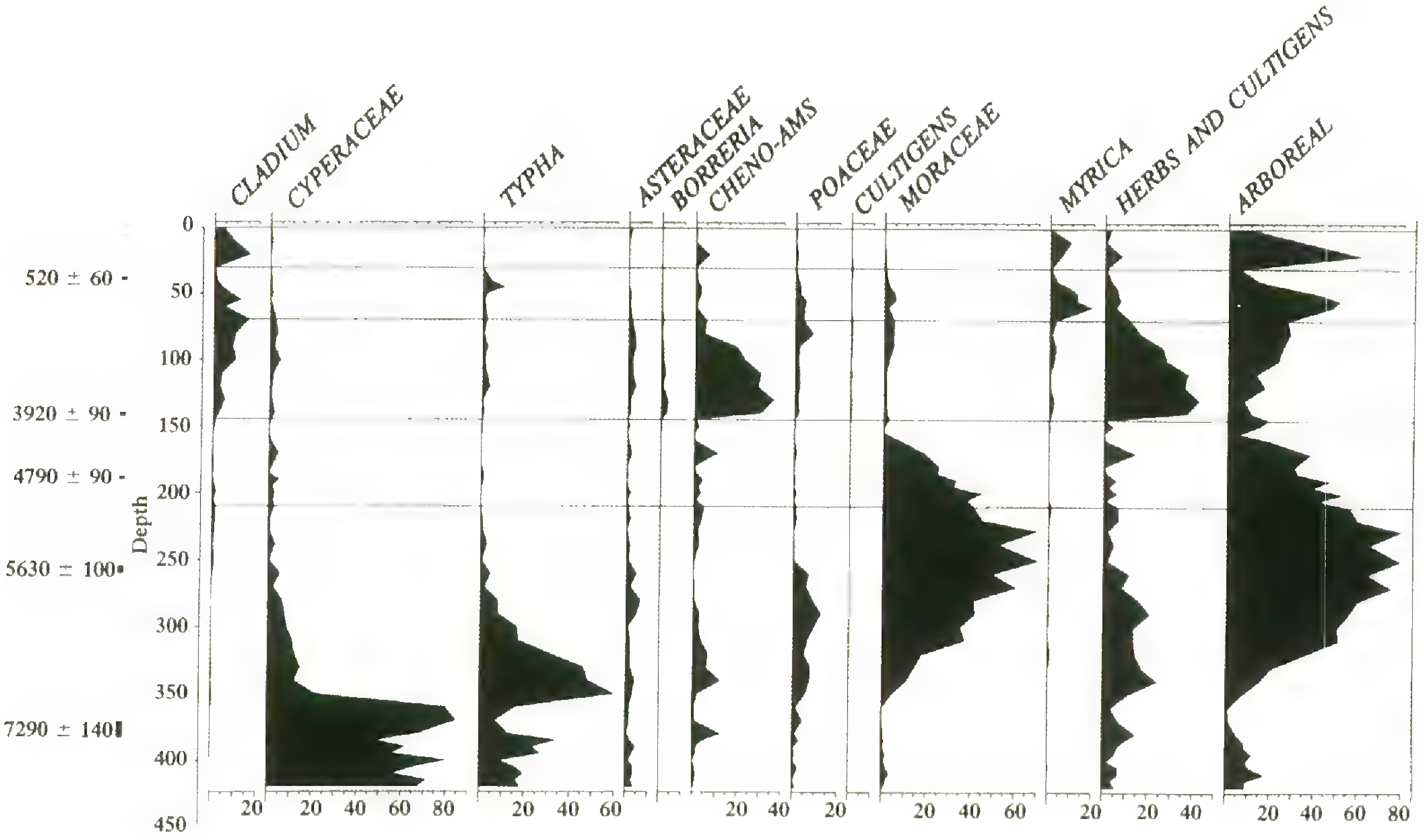

Figure 8. A pollen profile (percentage abundance of pollen at depth in cm below surface; age in ^{14}C yr. BP) from Cobweb Swamp, Belize. Cultigens are maize, cotton (*Gossypium* L. (Malvaceae)), and chile pepper (*Capsicum* L. (Solanaceae)). Taxa attributions are as follows: *Cladium* P. Browne (Cyperaceae), *Borreria* G. Mey (Rubiaceae). Reproduced with permission from Jones (1991).

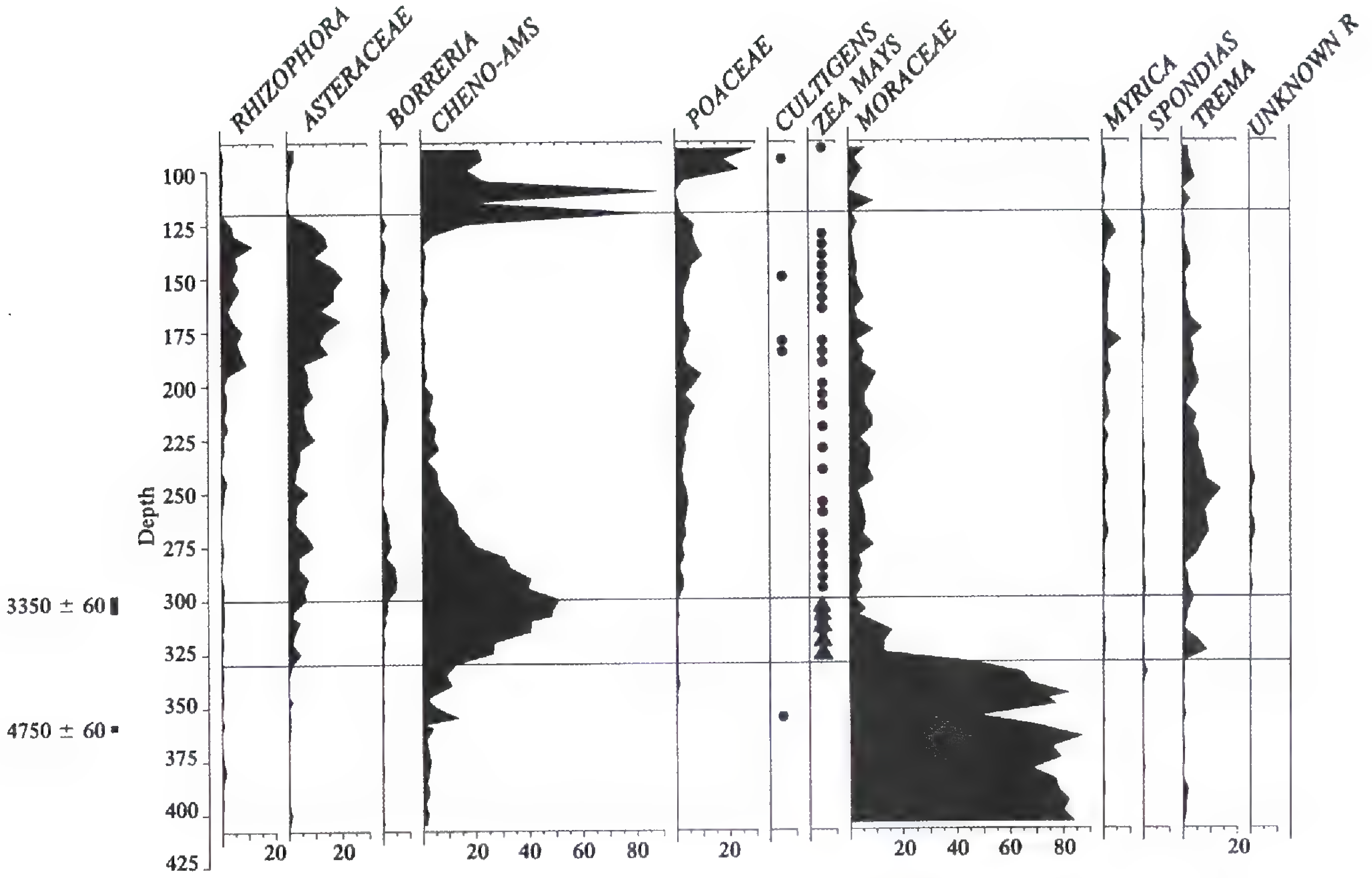

Figure 9. A pollen profile (percentage abundance of pollen at depth in cm below surface; age in ^{14}C yr. BP) from Kob Swamp, Belize. Cultigens are manioc (*Manihot esculenta* Crantz (Euphorbiaceae)) and cotton. Reproduced with permission from Jones (1994).

of this diversity is pre-Quaternary, perhaps dating to the Eocene (Knapp & Mallet, 2003; Wilf et al., 2003), although recent investigations also show that some tree species of Central and South American seasonally dry forest along with speciose genera of evergreen and other forests in South America probably did speciate during the past few million years (Richardson et al., 2001; Pennington et al., 2004). Whether those speciations occurred in refugia, islands of intact, lowland moist forest surrounded by savannas (Haffer, 1969; Whitmore & Prance, 1987), has not been completely resolved. However, interpretations of Late Pleistocene vegetation that rely on refugial theory appear increasingly less plausible as more paleoecological data accumulate indicating that due to drier conditions postulated refugial areas were nearly devoid of trees, or that these areas contained many colder-adapted taxa presently confined largely to montane forests (Colinvaux et al., 2000; Knapp & Mallet, 2003; Leyden, 1984, 1985).

It is relevant with respect to refugial theory that phytolith evidence from Monte Oscuro, Panama, discussed above, located in a highly seasonal area that was sparsely forested during the Pleistocene, does point to the presence of a number of lowland forest trees such as *Protium* and other Burseraceae, Annonaceae, Chrysobalanaceae, and Moraceae near the lake during the driest times before 10,000 BP There were almost certainly other tree species present there and at other similar locations that for various reasons (low pollen productivity or an absence of identifiable phytoliths) are not visible in the paleobotanical records. Some arboreal species may, therefore, have grown in lower densities than is usual today in more mesic pockets on the drier Pleistocene landscapes; for example, they may have been harbored alongside water courses. Studies of modern riparian forests by Meave and Kellman (1994) and others have shown that these linear stretches of vegetation contain a much greater diversity of tree species than was previously thought possible. Sir Ghillean Prance's (1987) idea that riparian forests were important refuges for lowland forest trees in Amazonia thus has considerable merit, and his view applies equally well to Central America. These findings and ideas on the historical significance of riverine forests should also be remembered by modern planners when they are considering what the sizes, shapes, and species composition of modern reforestation programs should be.

We've learned that the questions we first asked of the historical records—was the Pleistocene vegetation a forest or was it a grassland; were the lowland tropics cooler, or were they drier during an ice age; where did trees go during periods when savannas and scrub lands appear to have dominated landscapes now underneath forest? —were far too simplistic. We have begun to consider more realistic, if increasingly

complicated, Pleistocene scenarios involving the likelihood of different forest facies; the existence of species combinations not presently found together; heterogeneous, even patchy, vegetation across small distance scales; and stretches of forest alongside water courses in regions where forests were significantly reduced that may have held and preserved at least some of the diversity we see today during the past few million years. On average, glacial periods last four to five times longer than interglacials. Hence, during the past two million years, tropical forest plants and animals spent over 80% of their time in, and must have been well accustomed to, a world of lower CO_2, temperature, and precipitation. Our modern, closed canopied forests appear to be little more than short-term, interglacial floristic associations that coalesced or expanded onto landscapes the last time beginning 11,000 to 10,000 years ago. If the past is indeed the key to the present, then what we have learned about tropical forest history should cause us to look to ancient records for advice concerning, among other things, modeling plant succession following major ecosystem disruptions and predicting and patterning forest regeneration when planning regrowth programs (see also Birks & Birks, 2004, and Wardle et al., 2004).

Pre-Columbian Human Impacts on the Neotropical Forest

During the final 1000 years or so of the Pleistocene, the climate warmed markedly and became substantially wetter and more highly seasonal, and atmospheric concentrations of CO_2 increased, creating conditions in which tropical plants could really flourish. Humans had already arrived in Central and South America by at least 3000 years earlier, as demonstrated by Dillehay's (1997) excavations at Monte Verde, Chile. This work, which overturned the Clovis First paradigm for human colonization of the New World, is accepted as convincing proof of a 13,000 BP human presence in southern South America by a strong consensus of American archaeologists (Meltzer, 1997). At the close of the Pleistocene the human occupants of Central and South America, having spent the late glacial period in cool and dry landscapes where the amount of forest cover was far less than it is today and large, slow-moving, now-extinct game animals abounded, found themselves in surprising and dramatically changing ecological circumstances. Tropical forests, with their far fewer and much smaller animals and more highly dispersed and toxic plant species, were expanding rapidly on landscapes, and new strategies for living in these habitats would become necessary in fairly short order. One cultural adjustment to the changing ecological circumstances that turned out to be a highly successful adaptation was plant food production.

The transition from a hunting and gathering way of life to one in which human societies became dependent on a food base underwritten by plants they domesticated was accomplished independently in at least eight regions of the Old and New World, including both hemispheres of tropical America, not long after the Pleistocene ended (Diamond, 2002; Piperno & Pearsall, 1998; Kennett & Winterhalder, 2006). It marked the emergence of humans as owners and extraordinary manipulators of their landscapes. In southern Central and northern South America, the best studied regions to date, microfossil (phytolith, starch grain, and pollen) research indicates that the domestication and spread of important native crops like maize, manioc (*Manihot esculenta* Crantz), two species of squash (*Cucurbita moschata* Duchesne and *C. ecuadorensis* H. C. Cutler & Whitaker), arrowroot (*Maranta arundinacea* L.), yams (*Dioscorea trifida* L.f.), and líren (*Calathea allouia* (Aubl.) Lindl.) occurred between 10,000 and 5000 years ago (Bray, 2000; Mora et al., 1991; Pope et al., 2001; Piperno, 2006a; Piperno & Pearsall, 1998; Piperno & Stothert, 2003; Piperno et al., 2000a, b; Pearsall et al., 2003, 2004). Furthermore, together with evidence from molecular biology and botany, this tells us that the most important lowland crops in both Central and South America were originally brought under cultivation and domesticated in the seasonal, not the ever-wet tropical forest, and that the interior of the Amazon Basin had little at all to do with the origins of major subsistence crops (e.g., Matsuoka et al., 2002; Olsen & Schaal, 1999; Piperno & Pearsall, 1998; Piperno, 2006a; Sanjur et al., 2002; Westengen et al., 2005).

Paleoecological data from lakes and large swamps often located near important archaeological sites make it clear that the development and spread of agriculture in the American tropics exerted profound influences on the structure and composition of the vegetation. The numbers of sequences showing human agricultural and other alterations of the lowland tropical forest in Central America during the early and middle Holocene are rapidly increasing, and not all of them can be considered here. It is briefly noted that in addition to the records discussed below, good data also exist from Costa Rica, El Salvador, and coastal Guatemala, as well as from Puerto Rico (see, for example, Clement & Horn, 2001; Dull, 2004; Horn & Sanford, 1992; Arford & Horn, 2004). Virtually everywhere the records show that fire was an important instrument of vegetational modification for hunters and gatherers and people practicing agriculture alike.

At Lake La Yeguada in Panama, a disturbance horizon indicating frequent firing of the forest and small-scale vegetation clearance begins at 11,000 BP after being absent for the first 3000 years of the lake's history, when the climate was much drier (Piperno et al., 1990; Bush et al., 1992; Fig. 5a). The disturbance is represented by a large (several orders of magnitude) and rapid increase of charcoal and plants of forest gaps such as *Heliconia* and grasses, and it is sustained throughout the early Holocene. The initial appearance of the vegetation disturbance coincides with the settlement of the region by Clovis hunters and gatherers. These and later populations who occupied the La Yeguada watershed between 11,000 and 10,000 BP left numerous characteristic stone artifacts, including a projectile point on the shore of the lake itself, that have been found by archaeologists during systematic surveys (Ranere & Cooke, 2003).

More than 70% of the disturbance taxa phytoliths are continually charred from 11,000 to 9000 BP, providing direct indications that they had been fired repeatedly (burnt phytoliths can be easily recognized because they acquire a black coating on their surface; see Piperno, 2006b). Such a scenario would be highly unlikely under burning caused by natural processes because fire return rates in tropical forests documented for the modern era are never that frequent (at La Yeguada, the sampling resolution was often about 100 years). Furthermore, ENSO became a part of the post-Pleistocene climate system only after 6000 to 5000 BP (Moy et al., 2002; Sandweiss et al., 1996), and thus persistent fire events during the early Holocene cannot reasonably be attributed to El Niño dry periods. Hence it appears that early hunters and gatherers repeatedly subjected the forest around La Yeguada to fire and small-scale clearing.

The disturbance at La Yeguada continued unabated and intensified. Then at 7000 BP a marked decline in arboreal and associated species characteristic of older forest growth (which the phytolith record is more adept than pollen at identifying) and continued high frequencies of charcoal indicate the development of slash and burn cultivation. Pollen data, which are very sensitive to a set of woody secondary forest taxa generally not visible in phytolith profiles, such as *Trema*, *Pilea* Lindl., *Ficus* L., and *Cecropia* Loefl., indicate a concurrent substantial increase of such trees (Fig. 5b), confirming the decline in older forest growth recorded by the phytoliths. At 4000 BP, even these pollen types decline greatly, as does charcoal, indicating that an intensification of forest clearance occurred and not many woody taxa were left in the watershed (Fig. 5a, b). Also starting at ca. 7000 BP, when the earliest clear indications of slash and burn cultivation begin, nearby archaeological sites contain

Figure 10. Map of the Central Balsas watershed of Mexico showing the Iguala Valley (grey shading) and coring locations El Venancio and Las Juntas de Río Chico. Tehuacan Valley and Guila Naquitz are archaeological settlements located in the dry highlands where previous research has documented early food production.

the first phytoliths and starch grains from maize and manioc. These records show that crops such as arrowroot and *Cucurbita moschata* were also present by that date (Piperno, 1988, 2006a; Piperno et al., 2000b; Piperno & Pearsall, 1998).

At about 350 BP, when Europeans are known to have first entered the region, a forest resurgence is evident at La Yeguada. It is almost certainly a result of the terrible decimation of indigenous populations that occurred soon after the Spanish contact on account of disease, warfare, and slavery. Hence, the forests around La Yeguada were resilient to long-term prehistoric agriculture. Even so, some of the trees first recorded during the early Holocene do not appear again when indigenous population pressure decreases (e.g., *Protium*), while other taxa, especially forest floor herbs such as the Marantaceae, appear to be present in higher frequencies than they were before the vegetation was fired and cleared.

Similar early manifestations of human firing and clearing of tropical forest have been demonstrated from Mesoamerica to the Amazon Basin. For example, two pollen and charcoal records studied by John Jones from swamps called Kob and Cobweb, located about 55 km apart in northeastern Belize, show an early phase of intensive deforestation resulting from slash and burn agriculture (Jones, 1994; Pohl et al., 1996; Figs. 8, 9). The sites are near major pre-Classic archaeological occupations, and in both cases tree pollen greatly declines and maize is present by 4000 BP At this time, there are also sudden, major increases of charcoal fragments (not shown) and early successional herbaceous taxa. Among arboreal taxa, even pollen from *Brosimum* Sw. nearly disappears, indicating that the fruit of this tree, called *rámon*, probably was not a primary food source for Classic

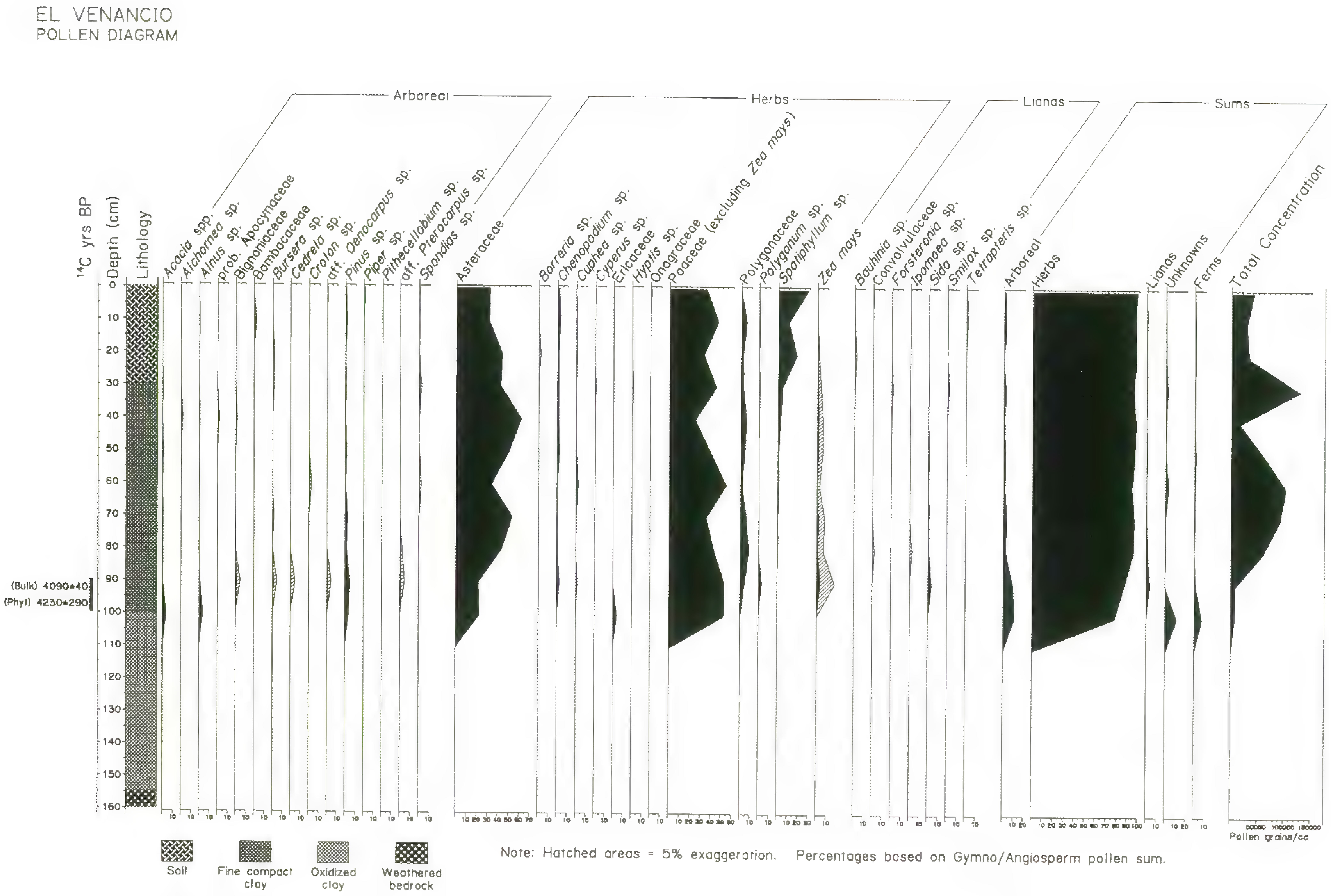

Figure 11. The percentage abundance of pollen of each taxon found in El Venancio, Mexico. Taxa attributions are as follows: *Acacia* L., *Pithecellobium* Mart., and *Pterocarpus* Jacq. (Fabaceae); *Alchornea* Sw. and *Croton* L. (Euphorbiaceae); *Cuphea* P. Browne (Lythraceae); *Cyperus* L. (Cyperaceae); *Forsteronia* G. Mey. (Apocynaceae); *Hyptis* Jacq. (Lamiaceae); *Ipomoea* L. (Convolvulaceae); *Pinus* L. (Pinaceae); *Piper* L. (Piperaceae); *Polygonum* L. (Polygonaceae); *Sida* L. (Malvaceae); *Smilax* L. (Smilacaceae); *Spathiphyllum* Schott (Araceae); *Tetrapteris* Cav. (Malpighiaceae).

Maya peoples, as was thought before Jones's pollen work and other studies showed otherwise (Jones, 1994). As in central Pacific Panama, the fertile soils of northern Belize were able to sustain intensive cultivation for thousands of years. Agricultural activity stops at about the time of European Contact at the Belize sites, but in those cases the forest did not recover. The reasons why are presently unclear.

The seasonal tropical forest of the Río Balsas drainage of Mexico appears, based on molecular studies of modern crops and their nearest wild relatives, to have been an important center of crop plant origins, where maize, the silver-seeded squash (*Cucurbita argyrosperma* Huber), and other plants were domesticated (Matsuoka et al., 2002; Sanjur et al., 2002). However, very little archaeological or paleoecological research has been undertaken there, owing largely to the fact that investigators long assumed that crop plant evolution largely occurred in the dry mountainous zones of the country. Therefore, virtually nothing is known of the earlier segments of pre-Columbian human history (ca. 12,000 BP to 3000 BP) in the Balsas watershed. During the past five years, the author has directed reconnaissance and coring of lakes and swamps in the Central Balsas region, where the modern populations of *Zea mays* subsp. *parviglumis* are genetically closest to maize (Matsuoka et al., 2002; Fig. 10). The Iguala Valley and its environs, located in Guerrero on the eastern side of the Central Balsas drainage, appears to have been a smaller-scale version of the lake district in the Petén, Guatamala, as there are large lakes and numerous other basins that held permanent water until recently (Piperno et al., 2004). The sequences from two of these sites, which date to the Late Pleistocene, are still being investigated in the author's laboratory and cannot yet be discussed in detail.

In the Central Balsas watershed, about 120 km west of Iguala near the town of Ciudad Altamirano, still in Guerrero but close to the border of Michoacán, one large swamp and the remnants of an oxbow lake were located and cored. These sites are called, respectively, El Venancio and Las Juntas de Río Chico (Fig. 10). The elevation of the area is 300 m asl, and annual precipitation is about 1400 mm. The potential vegetation is tropical deciduous forest, but the region is apparently too low-lying and warm to support the growth of teosinte, which has never been collected there. A 1.6 meter-long sequence retrieved from El Venancio has two concordant dates of 4090 ± 40 BP and 4230 ± 290 BP obtained, respectively, from sediments and phytoliths retrieved from the same sediments at a depth of between 90 and 100 cm beneath the surface (b.s.) (Fig. 11). There and up the core to about 30 cm b.s., sediments are dark, organic-rich, silty clays containing abundant pollen grains and phytoliths. Beneath 100 cm, sediments are organic-poor clays largely devoid of any plant material.

The pollen analysis, carried out by Enrique Moreno of the Smithsonian Tropical Research Institute, shows that by 4000 BP the vegetation contained few trees and was instead dominated by early successional plants indicative of landscape clearing, such as the Poaceae and Asteraceae (Fig. 11). Maize pollen occurs at that time (and is present continually throughout the later portions of the sequence), along with abundant fragments of charcoal (not shown). This picture is repeated at nearby Las Juntas de Río Chico (Fig. 12). Here, a 1.5 meter-long sedimentary sequence shows that the same taxa indicative of landscape clearing present at El Venancio by 4000 BP dominate the pollen assemblages found at a depth of 110 to 120 cm b.s., dated to 3050 ± 40 BP Maize pollen and abundant charcoal particles occur here. Sediments beneath 120 cm b.s. contain relatively few pollen grains, making it difficult to interpret the vegetation with the degree of confidence possible in stratigraphically higher deposits. It can be said that the basal-most pollen, which on the basis of estimates derived from sedimentation rates probably dates to about 4000 BP, is mostly from grasses, and there is no large spike of fern spores that would indicate differential degradation of pollen grains (the pine pollen is almost certainly a result of long distance transport). Importantly, there are also abundant charcoal particles in the deepest sediments.

We thus have our first indications that in the Central Balsas region, thought now to be a cradle of agriculture in Mesoamerica and the hearth of maize, agricultural systems using maize that resulted in intensive forest clearing have considerable antiquity. The few trees and lianas remaining on the landscape at 4000 BP (*Cedrela* P. Browne, *Spondias*, Bombacaceae, *Bauhinia* L., palms such as *Oenocarpus* Mart.) provide but a small hint of the species-rich forest that existed before humans burned and cleared the vegetation.

A discussion of the South American paleoecological records that speak to ancient human modification of the environment for agricultural and other practices is beyond the scope of this paper. However, one important pollen record studied by the prominent Colombian paleoecologist, Luisa Herrera, and her colleagues should be mentioned (Mora et al., 1991). The sequence comes from the wet evergreen forest of the now-remote middle stretches of the Rio Caquetá in the center of the Colombian Amazon (annual precipitation > 3000 mm). It shows clearly that by 4700 BP a slash and burn system of agriculture using maize, manioc, and other crops was well established

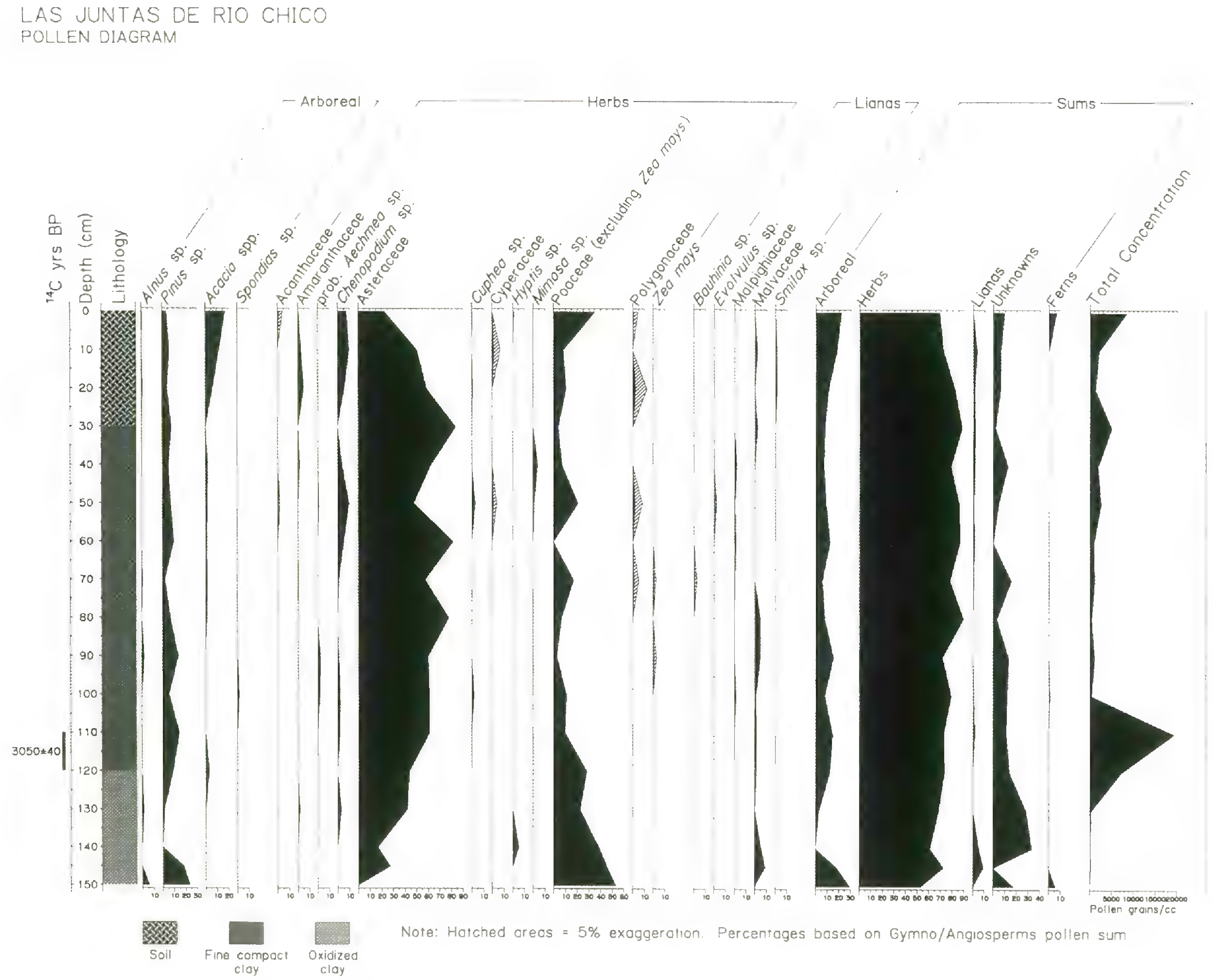

Figure 12. The percentage abundance of pollen of each taxon found in Las Juntas de Río Chico, Mexico. Taxa attributions are as follows: *Aechmea* Ruiz & Pavón (Bromeliaceae); *Evolvulus* L. (Convolvulaceae); *Mimosa* L. (Fabaceae).

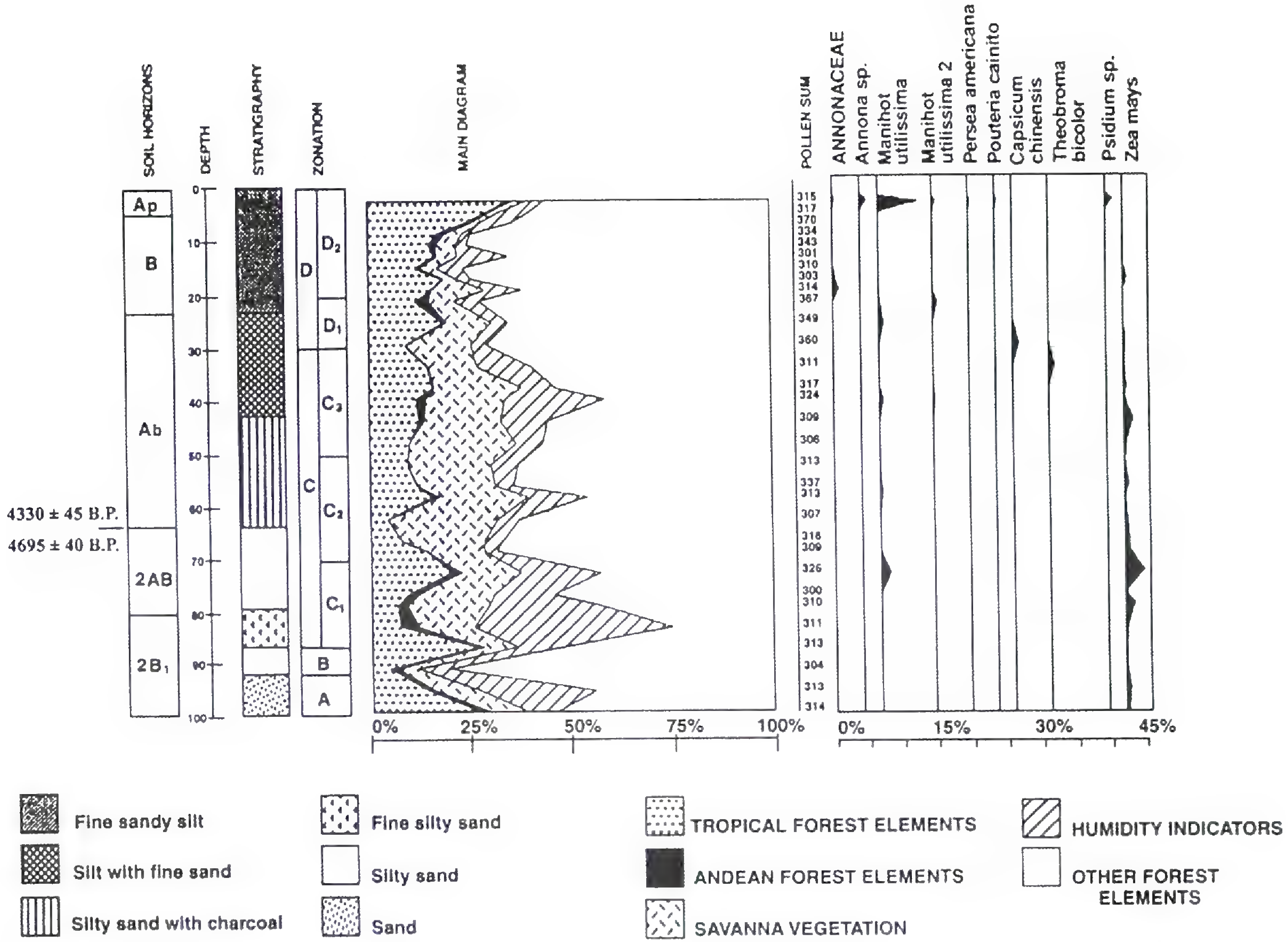

Figure 13. Pollen (the percentage of pollen of each taxon) and charcoal profiles found in the Río Caquetá region of the Colombian Amazon. Taxa attributions are as follows: *Annona* L. (Annonaceae), *Manihot utilissima* Pohl (Euphorbiaceae), *Persea americana* Mill. (Lauraceae), *Pouteria cainito* (Ruiz & Pavón) Radlk. (Sapotaceae), *Capsicum chinense* Jacq. (Solanaceae), *Theobroma bicolor* Bonpl. (Sterculiaceae), *Psidium* L. (Myrtaceae). Reproduced with permission from Mora et al. (1991).

(Fig. 13). By this time, grasses and other field weeds had supplanted the species-rich forest. As in the Central American sequences, presence of abundant fragments of charcoal at 4700 BP testify that fire played an important role in field preparation. At about 775 years ago, when associated archaeological data indicate the site was abandoned by its human occupants, higher frequencies of trees returned and burning ceased. This record from the Colombian Amazon can be contrasted to those from three distinct watersheds in the "Hill of Six Lakes" region, located in wet evergreen forest in northern Brazil where annual precipitation is greater than 3000 mm (Colinvaux et al., 1996; Bush et al., 2004). These sequences demonstrate that few forest fires and no recognizable human vegetational modification occurred in the area during a very long time period stretching from more than 40,000 years ago to the modern era.

Sauer (1958) argued that humankind's successful adaptation to the tropical forest, especially the seasonally dry one, was aided greatly by the use of fire. He presciently predicted that because Neotropical trees are thin-barked and thus poorly insulated, having had apparently a short evolutionary history with fire, early hunters and gatherers and farmers alike could use fire as a highly effective tool for exploiting the forest. This made it possible to kill trees easily and create substantial openings or enlarge existing open areas without having to depend on a sophisticated stone tool technology (Sauer, 1958). In Panama, the Colombian Amazon, and other areas not discussed here where paleoecological records testify to the appearance of slash and burn cultivation several millennia and more ago, associated archaeological data indicate that stone axes were not commonly used before 3000 BP (Piperno & Pearsall, 1998).

Summary: What Have We Learned about Ancient Human Impacts on Neotropical Vegetation?

Human cultures had profound effects on the structure and composition of the lowland tropical forest long before Europeans arrived. Human-induced perturbations were often greater and more widespread than those brought about by Pleistocene climatic and other physical factors. Many arboreal and even herbaceous taxa were in large or smaller part removed from landscapes that were underneath indigenous agricultural systems. Other plants experienced range extensions as they were widely dispersed together with crop plant species, or were otherwise exchanged between human cultures, experimented with, and grown outside of their native habitats. Existing records also suggest that different species and plant communities had contrasting regenerative capacities following severe disruption, as they do today. Without paleoecological data it might be difficult to know how much of any extant forest was truly very old or not an artificial product of human intervention and subsequent abandonment.

Although we now understand that early peoples substantially altered their landscapes, we should not assume that every tract of lowland tropical forest was heavily settled and disturbed during the prehistoric era. With little doubt, variability in land use patterns resulting from the inherent fertility of soils, type of agriculture practiced (root/tree- vs. seed-based), and associated human population densities resulted in differential impacts on vegetation. The contrasting records from the Hill of Six Lakes in Brazil and the Río Caquetá region of the Colombian Amazon discussed above are but two examples (see Piperno & Becker, 1996, and Bush et al., 2000, for three others from the Brazilian Amazon).

The timing and duration of landscape modification would also have varied depending on whether a region was a cradle of crop plant evolution or otherwise witnessed early developments of agricultural systems through participation in the initial dispersals of domesticated plants, as occurred in Central Pacific Panama, for example. One might suspect, then, that highly seasonal tropical forests, which on present evidence were the geographic cradles of origin for many staple seed and root crops of the Neotropics, were more greatly affected over more protracted time scales than were forests in wet, aseasonal, and poorly soiled regions. While these are reasonable suggestions that accord well with available information, data from many regions are still few and there is much to be learned.

Unlike the thinking that prevailed in human studies little more than 20 years ago, many anthropologists now decline to argue that modern land use practices in the tropics by small-scale, politically autonomous indigenous societies preserve or increase plant diversity, or that there is an inherent conservation ethic that simpler human societies still adhere to (see Alcorn, 1996, Redford & Padoch, 1992, and Alvard, 1995, for good discussions of these issues). I doubt that these ideas constitute accurate assessments of human relationships with, and impacts on, natural resources at any moment in time. None of the now substantial paleoecological records indicate they were true in the past. If Europeans had not arrived little more than 500 years ago and tragically all but ended indigenous life in many areas of Central and South America, it is very much an open question as to how sustainable intensifying or even maintaining existing agricultural practices would have been under ever-

increasing human population densities, even with the use of relatively simple technologies (stone tools and fire) as instruments of forest clearing. Archaeological records from the tropics and elsewhere also tell stories of over-exploitation of marine and other resources during the prehistoric era (e.g., Jones et al., 2004; Mannino & Thomas, 2002; Porcasi et al., 2000; Stahl, 1996; Steadman, 1995). Moreover, rigorous studies of modern indigenous resource use in tropical South America make it clear that short-term self-interest and a desire to capture game in an energetically efficient manner structure hunting and other subsistence pursuits much more so than does a long-term interest in conserving resources (e.g., Alvard, 1993, 1995; Winterhalder & Lu, 1997).

In order to better preserve and protect the remaining forests, we have to straightforwardly assess past and present human behavior, its proclivities, and its goals. At the very least, we should more carefully define what we mean by the word conservation when we describe modern indigenous resource use (is it a designed attempt to preserve an existing biomass and diversity, or an epiphenomenal by-product of factors such as low human population and high prey densities?), no matter how sustainable the resource usage appears to be (see Alvard, 1993, and Smith & Wishnie, 2000, for excellent discussions of this issue).

Finally, there is little doubt now that the views originally taken by Donald Lathrap and Carl Sauer (Lathrap, 1970, 1973b; Sauer, 1936, 1947, 1950) concerning the importance of the lowland Neotropical forest in the emergence and spread of domesticated species, the development of effective agricultural systems, and the flourishing of cultural life in general, were correct in many aspects. In fact, as Lathrap had predicted, the origins of New World pottery occurred in the heart of Amazonia 7000 years ago (Roosevelt et al., 1991), and the first permanent, agricultural villages were created by people who lived in the seasonal forests of southwest Ecuador 5000 years ago (Lathrap et al., 1975; Pearsall et al., 2004). Newer explorations in the Brazilian Amazon have documented that beginning a few centuries before the time of Christ, very large, dense, and permanent human settlements existed in the middle to lower stretches of the main Amazon river channel and Upper Xingu region, which are now sparsely populated and under forest cover (Heckenberger et al., 1999, 2003). As with the forces associated with "development" today, these prehistoric advances probably came with negative consequences for the native flora and fauna. Profound human alteration of the tropical landscape with substantial loss of biodiversity is hardly new, but we are the first societies with the wherewithal to do something about it.

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THE PALEOBOTANICAL RECORD OF COLOMBIA: IMPLICATIONS FOR BIOGEOGRAPHY AND BIODIVERSITY[1]

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Abstract

Plant microfossil and macrofossil associations obtained from six dated sections from the area of the basin of Bogotá (2550 m, Eastern Cordillera, Colombia) show the evolution of the late Neogene Andean montane forest, triggered by the Andean orogeny. Progressive adaptation of warm tropical taxa to cool montane conditions, evolution of new neotropical montane taxa, and immigration of temperate Laurasian, Holarctic, and Austral-Antarctic elements gave shape to the present-day montane forest. Vegetational characteristics inferred from fossil plant associations reveal the altitude at the time of deposition. Neogene forests are floristically compared with contemporary forests at comparable altitudinal intervals in the surroundings of the Bogotá basin; however, the absence of taxa that had not yet arrived, or evolved, is most salient and shows that non-analogue plant communities are common.

The main phases of montane forest development are: (1) pre-uplift phase of the late Miocene with abundant lowland taxa with tropical or neotropical affinities (*Mauritia* Kunth, *Amanoa* Aubl., *Ceiba* Miller, and representatives of Humiriaceae); montane forest rich in Podocarpaceae (potentially including *Nageia* Gaertn., *Podocarpus* L'Hér., *Prumnopitys* Phil., and *Retrophyllum* C. N. Page) covered other previously uplifted areas in the region; (2) toward the early Pliocene the area was uplifted to ca. 1000 m; the relative proportion of temperate taxa of North American and southern South American stock increased and occupied the slopes of the low mountains; and (3) by the middle Pliocene uplift had proceeded to ca. 2000–2200 m and tropical lowland taxa, which are now restricted to altitudes below 1000 m, are no longer recorded in the fossil plant associations; the increase in the number of newly appearing montane taxa (*Myrica* L., *Turpinia* Vent., *Gunnera* L., *Bocconia* L., *Gaiadendron* G. Don f., *Daphnopsis* C. Martius, and *Monnina* Ruiz & Pav.) suggests a significant increase of diversity.

Until the late Pliocene there is little to no evidence for the existence of the páramo; taxa such as *Xyris* L., *Hypericum* L., *Carex* L., *Montia* L., and *Ranunculus* L. might have formed swamp or bog vegetation only. It is believed that these taxa colonized mountaintops with half-open vegetation; these areas extended when the mountains reached above upper forest line elevations.

The distribution areas of the endemic genera of the Espeletiinae largely coincide with the youngest parts (< 5 Ma) of the northern Andes. Changing climatic conditions forced individual plant species to migrate vertically. Composition of plant communities changed continuously and vegetation belts frequently were altitudinally squeezed or offered possibilities for expansion. This long process stimulated speciation and provoked sequential non-analogue vegetation types. Thus, the biodiversity hotspot of the northern Andes has a dynamic history.

Key words: Andean uplift, biome evolution, Colombia, Espeletiinae, montane forest, Neogene, páramo, phytogeography.

Resumen

Los microfósiles de plantas y asociaciones de macrofósiles obtenidos de seis secciones fechadas del área de la cuenca de Bogotá (2550 m, Cordillera Oriental, Colombia) demuestran la evolución del bosque andino del Neógeno tardío, accionado por la orogenia andina. La adaptación progresiva de taxones tropicales calidos hacia las condiciones frías montanas, la evolución de nuevos taxones neotropicales montanos y la migración de elementos templados laurásicos, holárticos y austral-antárticos dieron forma al bosque montano actual. Las características de la vegetación deducidas de las asociaciones de plantas fósiles revelan la altitud al momento de los depósitos. Los bosques neógenos se comparan florísticamente con bosques contemporáneos a intervalos altitudinales comparables en los alrededores de la cuenca de Bogotá; sin embargo, la ausencia de taxones que todavía no habían llegado, o desarrollado, es sobresaliente y demuestra que las comunidades de plantas no análogas son comunes.

Las fases principales del desarrollo del bosque montano son: (1) fase pre-levantamiento del Mioceno tardío con abundancia de taxones de las tierras bajas con afinidades tropicales o neotropicales (*Mauritia* Kunth, *Amanoa* Aubl., *Ceiba* Miller y representantes de Humiriaceae); un bosque montano rico en Podocarpaceae (potencialmente incluyendo *Nageia* Gaertn., *Podocarpus* L'Hér., *Prumnopitys* Phil. y *Retrophyllum* C. N. Page) cubría otras áreas previamente levantadas en la región; (2) hacia el Plioceno temprano el área se elevó ca. 1000 m; la proporción relativa de taxones templados de origen norteamericano y suramericano meridional aumentó y ocupó las vertientes de las montañas bajas; y (3) hacia el Plioceno medio, el

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levantamiento había llegado hasta ca. 2000–2200 m y taxones tropicales de las tierras bajas, que actualmente se restringen a las altitudes bajo los 1000 m, ya no se registran más en los registros fósiles de asociaciones de plantas; el aumento del número de taxones montanos nuevos (*Myrica* L., *Turpinia* Vent., *Gunnera* L., *Bocconia* L., *Gaiadendron* G. Don f., *Daphnopsis* C. Martius y *Monnina* Ruiz y Pav.) sugiere un aumento significativo de la diversidad.

Hasta el Plioceno tardío, hay poco a ninguna evidencia de la existencia del páramo; taxones como por ejemplo *Xyris* L., *Hypericum* L., *Carex* L., *Montia* L. y *Ranunculus* L. pudieron haber formado sólo vegetación de los pantanales o las turbas. Se cree que estos taxones colonizaron las cimas de las montañas con vegetación semi-abierta; estas áreas se extendieron cuando las montañas alcanzaron elevaciones sobre el límite superior del bosque.

Las áreas de distribución de los géneros endémicos de Espeletiinae coinciden en gran parte con las regiones más jóvenes (< 5 Ma) de los Andes del norte. Condiciones climáticas cambiantes forzaron a especies individuales de plantas a migrar verticalmente. La composición de las comunidades de plantas cambia continuamente y los cinturones de vegetación fueron comprimidos altitudinalmente o se ofrecieron posibilidades de expansión. Este largo proceso estimuló especiación y provocó tipos de vegetación secuenciales no análogos. Así el punto caliente de biodiversidad de los Andes del norte tiene una historia dinámica.

Increasing knowledge of the present-day flora and vegetation in the northern Andes promoted a simultaneous interest in its history. Paleoecological, primarily palynological, studies of Neogene sediments have provided a general understanding of the composition of the flora in the past and its changes over time. Van der Hammen et al. (1973) demonstrated the influence of tectonics and climatic change on the development of the Andean forest. Since then, understanding of how and when the present-day Andean forest acquired its floristic composition has increased by integrating paleodata with information about the present-day Andean forest (Raven & Axelrod, 1974; van der Hammen, 1974; Simpson, 1975; Gentry, 1982; Cleef et al., 1983; van der Hammen & Cleef, 1986; van der Hammen, 1989; Simpson & Todzia, 1990; Hooghiemstra & Cleef, 1995; Hooghiemstra & van der Hammen, 2004).

This paper focuses on results obtained from plant macrofossils and fossil pollen from sediments located in the basin and surrounding areas of Bogotá, Eastern Cordillera of Colombia. Sites are sections from outcrops or deep bore holes and are all located at ca. 2550 m (Fig. 1). Fossil plant assemblages from the late Miocene (sites Salto de Tequenedama I/II; Wijninga, 1996a), early Pliocene (site Río Frío; Wijninga, 1996c), middle Pliocene (site Subachoque-39; Wijninga & Kuhry, 1990; site Facatativá-13; Wijninga, 1996b), and late Pliocene (site Guasca; Wijninga & Kuhry, 1993) present snapshots of the long-term paleoecological development of the northern Andes (Table 1). Paleoecological data are compared with present-day northern Andean flora in core Fuquene-2 (van Geel & van der Hammen, 1973) to shed light on speciation, migration, plant diversity, and phytogeographic composition (Cleef, 1979; Cuatrecasas, 1979; van der Hammen & Cleef, 1986; Luteyn, 1999). In addition, a synthesis of these data is presented to support our understanding of how evolution of the Neogene sedimentary environment and vegetation in northwestern Amazonia relates to the uplift of the northern Andes.

The objective of the present paper is to compare the paleobotanical evidence from the northern Andes with paleobotanical studies from Amazonian lowland sediments in order to reconstruct the evolution of the northern Andean biota. The phytogeographic composition of the fossil plant assemblages shows snapshots of a long process of gradual change. Uplift created large areas of habitat that had previously not existed regionally, offering new establishment possibilities for floral elements from different source areas. The biostratigraphic position of the recorded plant taxa is evaluated.

Altitudinal Zonation of the Present-day North Andean Vegetation as a Basis for Paleo-reconstructions

The altitudinal zonation of the neotropical montane vegetation is primarily due to the effect of decreasing temperature with increasing elevation. Many studies have been dedicated to the composition and structure of the neotropical montane forest (e.g., Cuatrecasas, 1934; Grubb et al., 1963; van der Hammen & González, 1963; Vareschi, 1980; Cleef et al., 1983; Cleef & Hooghiemstra, 1984; Huber, 1986; Ulloa Ulloa & Jørgensen, 1993; Rangel, 1995; Rangel et al., 2003; Cleef et al., 2003). Cuatrecasas (1958) published an altitudinal zonation for the Colombian vegetation, later depicted by van der Hammen (1974) (Fig. 2). Their scheme of altitudinally arranged vegetation belts is used in this study, but new information from Wille et al. (2001) and Torres (2006) has been incorporated. This altitudinal zonation corresponds principally to the global vegetation zonation in high tropical mountains (Grubb, 1974, 1977) and is the basis for interpreting paleorecords in terms of uplift, climate change, and changing floristic compositions.

The following account of the present-day altitudinal vegetation distribution in the Eastern Cordillera of Colombia is needed to support the interpretation of

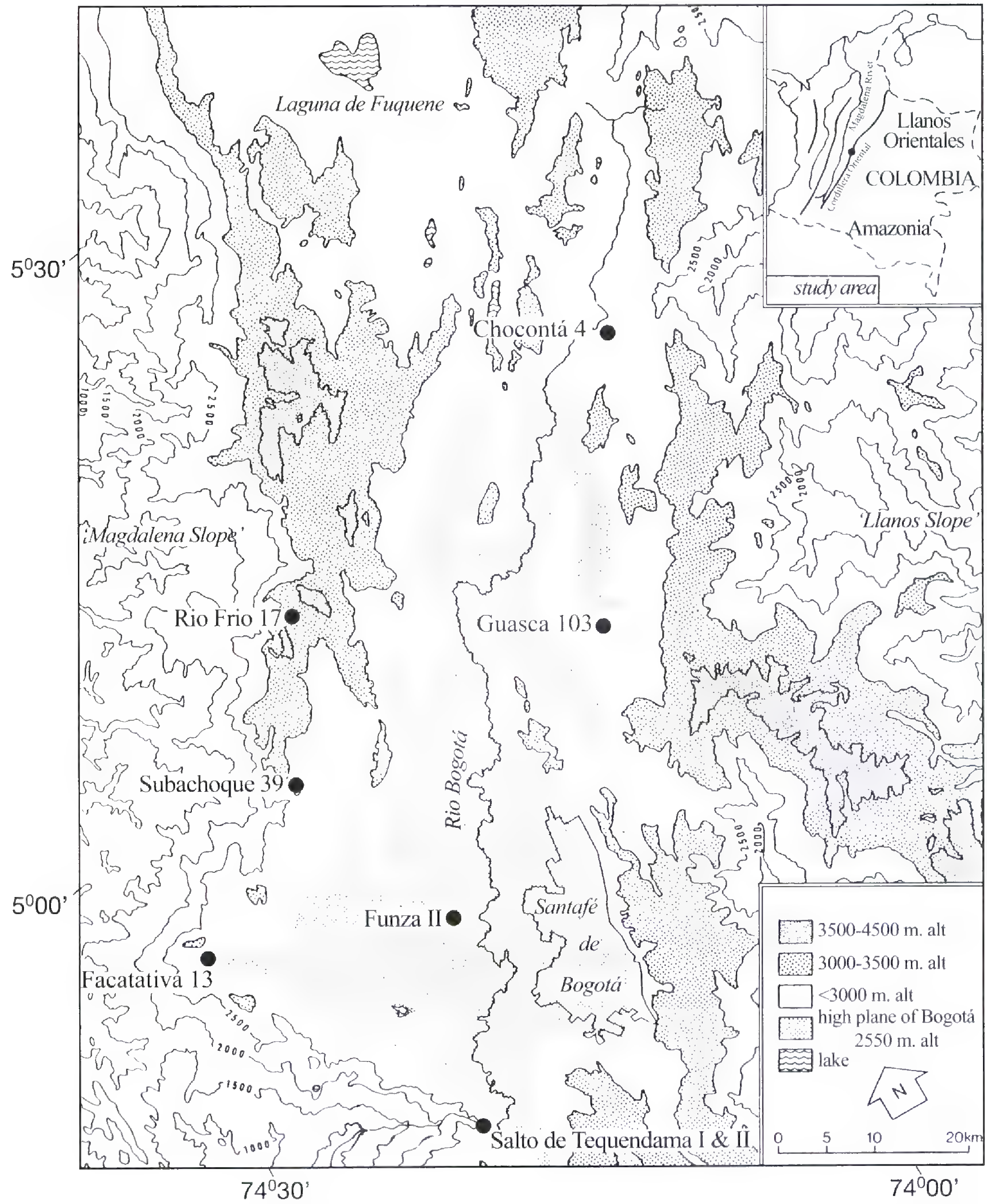

Figure 1. Map of the high plain of Bogotá, Colombia, and surroundings. Black dots indicate locations of sites (sections from outcrops and deep bore holes) with sediments of an age from late Miocene to late Pliocene. Modified after Hooghiemstra (1984), reprinted with permission from E. Schweizerbart'sche Verlagsbuchhandlung.

fossil assemblages in paleoaltitudes. Here we use the family level because a significant proportion of pollen- and macrofossil taxa were identified to that level. Moreover, given our objectives, Keizer's (2000) vegetation analysis of the Colombian Eastern Cordillera indicates that analysis at the family level is sufficient. During the Miocene and Pliocene, individual taxa may have had slightly different altitudinal ranges compared to today (Torres, 2006; Torres & Hooghiemstra, in prep.), but the large number of taxa used to infer paleoaltitudes and the relatively large envelope of uncertainty associated with the paleoaltitude estimates compensate for such potential taxa-specific errors.

Table 1. Site-specific data of sections and cores in and around the basin of Bogotá, Colombia, used in this study (see Fig. 1).

Site	Salto de Tequendama I (section)	Salto de Tequendama II (section)	Río Frío 17 (section)	Subachoque 39 (section)	Facatativá 13 (section)	Guasca 103 (section)	Fuquene 2 (core)	Funza 1 (core)	Funza 2 (core)
Coordinates	4°50′N, 74°20′W	4°50′N, 74°20′W	5°14′N, 74°29′W	5°06′N, 74°29′W	4°57′N, 74°33′W	5°13′N, 74°15′W	5°27′N, 73°46′W	4°50′N, 74°12′W	4°59′N, 74°22′W
Modern altitude (m)	2450	2475	3165	2820	2750	2650	2580	2550	2550
Lithostratigraphy	Lower Tilatá Formation/ Tequendama Member	Lower Tilatá Formation/ Tequendama Member	Lower Tilatá Formation/ Tibagota Member	Lower Tilatá Formation/ Tibagota Member	Lower Tilatá Formation/ Tibagota Member	Upper Tilatá Formation/ Guasca Member	—	—	—
Depositional environment	stream deposit, river channel	floodplain, swamp	stream deposit, lake	floodplain deposit	peat, swamp, lake	swamp, lake	lake	swamp, lake, river deposits	swamp, lake, river deposits
Sample interval (m)	34.70–34.75/ 35.15–35.20	1.20–1.25	0.60–0.65	0.35–0.40	1.90–1.95	26.75–26.80	12–0	357–0	586–0
Sample material	peaty silt	peaty clay	silt	peaty silt	peat	peat	(peaty) clay, peat	clay, sandy clay, peat	clay, sandy clay, peat
Main macroremains	wood, cuticles	cuticles	seeds	wood	wood, cuticles	cuticles	—	—	—
Age (Ma)	± 17–11	± 17–11	5.3 ± 1	± 5–4	3.7 ± 0.7	± 3	ca. 32–0 ka	ca. 1.6 Ma–30 ka	ca. 3.2 Ma–30 ka
No. of taxa included in percentage calculations	63	63	18	52	59	32	—	—	—
Biozone	I	I	II	II	II	III	VII	V, VI, VII	IV, V, VI, VII
Inferred paleoaltitude (m)	< 700 (± 500)	< 700 (± 500)	ca. 1000 (maximally ca. 1500)	1000 (± 500)	2000 (± 500)	2200 (± 500)	—	—	—
References	Wijninga, 1996a; 1996d	Wijninga 1996a; 1996d	Wijninga, 1996c; 1996d	Wijninga & Kuhry, 1990; Wijninga, 1996d	Wijninga, 1996b; 1996d	Wijninga & Kuhry, 1993; Wijninga, 1996d	van Geel & van der Hammen, 1973	Hooghiemstra, 1984, 1989; Andriessen et al., 1993; Torres, 2006	Andriessen et al., 1993; Torres et al., 2005; Torres, 2006
Relevance	1	1	1	1	1	1	2	3	4

1. Paleoflora from which paleoaltitude has been inferred.
2. Modern flora used for comparison with paleofloras.
3. Pollen spectra reflect Quaternary setting after the upheaval of the Eastern Cordillera was completed.
4. Pollen spectra reflect late Pliocene and Quaternary setting after the upheaval of the Eastern Cordillera was completed.

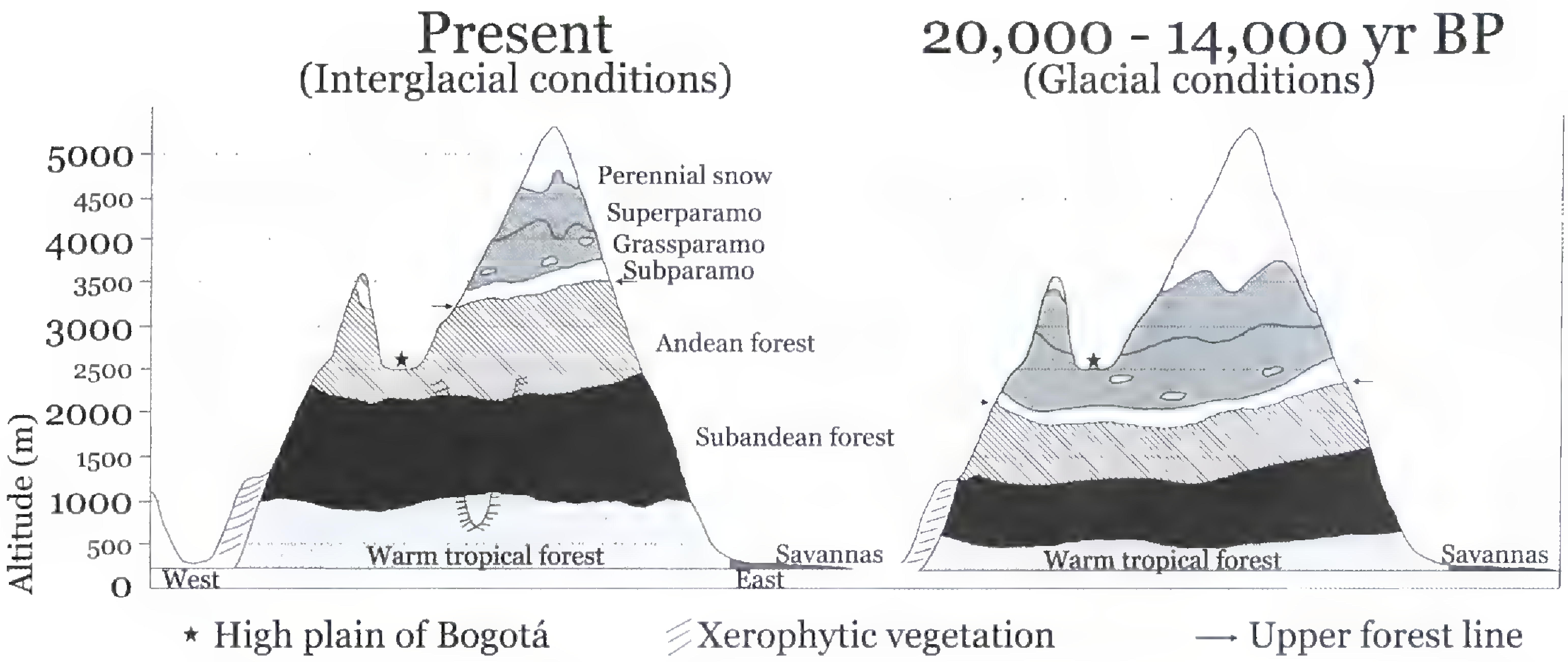

Figure 2. Schematic cross section through the Eastern Cordillera at the latitude of Bogotá. The altitudinal distribution of zonal vegetation belts for the present and the Last Glacial Maximum are shown. Xerophytic vegetation is mainly azonal and occurs in the interandean valleys. Its presence is shown because xerophytic elements are also present in the associations of paleofloras of this study. Modified after van der Hammen (1974), reprinted with permission from Blackwell Publishing.

The present-day tropical lowland belt extends from sea level to 1000–1200 m, and annual temperatures average 30°C at the lower altitudinal limit to 24°C at the upper altitudinal limit. The vegetation is principally characterized by arboreal representatives of the Anacardiaceae, Annonaceae, Apocynaceae, Arecaceae, Bombacaceae, Burseraceae, Caryocaraceae, Cecropiaceae, Clusiaceae, Euphorbiaceae, Humiriaceae, Lauraceae, Lecythidaceae, Leguminosae, Melastomataceae, Meliaceae, Moraceae, Myristicaceae, Rubiaceae, Sapotaceae, Sterculiaceae, Tiliaceae, and Vochysiaceae. Savanna vegetation is dominated by Poaceae and characterized by woody genera including Dilleniaceae, Malpighiaceae, and Rubiaceae. The most species-rich families include Fabaceae, Myrtaceae, Orchidaceae, Piperaceae, Rubiaceae, and Sapindaceae.

The present-day subandean forest belt (= lower montane forest belt) extends from 800–1200 to 2300–2500 m, and average annual temperatures are from 24°C at the lower altitudinal limit to 16°C at the upper altitudinal limit. Common arboreal taxa include representatives of the Araliaceae, Arecaceae, Brunelliaceae, Cecropiaceae, Clusiaceae, Cyatheaceae, Euphorbiaceae, Fabaceae, Fagaceae, Hippocastaneaceae, Lauraceae, Malpighiaceae, Melastomataceae, Meliaceae, Proteaceae, Rubiaceae, Rutaceae, and Solanaceae. The most species-rich families include Leguminosae, Orchidaceae, Polypodiaceae, Rubiaceae, and Solanaceae.

The present-day Andean forest belt (= upper montane forest belt) extends from 2300–2500 to 3200–3300 m, and annual temperatures average 16°C at the lower altitudinal limit to 9°C at the upper altitudinal limit. The upper altitudinal limit reflects the upper forest line. Palynological studies from deep cores from the basin of Bogotá show that during the Pliocene the upper forest line corresponded to a higher temperature than today (Hooghiemstra, 1984; Torres, 2006; Torres & Hooghiemstra, in prep.). Therefore, the Miocene-Pliocene temperature range may have been ca. 16°C to ca. 11°C. Common families are Aquifoliaceae, Araliaceae, Betulaceae, Caprifoliaceae, Chloranthaceae, Clethraceae, Clusiaceae, Cunoniaceae, Cyatheaceae, Elaeocarpaceae, Ericaceae, Euphorbiaceae, Fagaceae, Juglandaceae, Loranthaceae, Melastomataceae, Myricaceae, Myrsinaceae, Myrtaceae, Arecaceae, Proteaceae, Rosaceae, Solanaceae, Symplocaceae, Theaceae, Thymelaeaceae, and Winteraceae. The most species-rich families include Asteraceae, Ericaceae, and Polypodiaceae.

The present-day subpáramo zone is immediately above the upper forest line and extends from 3200–3300 to ca. 3600 m, and annual temperatures average 9°C to 7°C at its upper limit. The lower part of the subpáramo belt is dominated by shrub and dwarf forest, whereas the upper part is characterized by dwarf shrub vegetation. The pollen record of Funza-2 shows that the subpáramo belt developed further during the late Pliocene (Torres, 2006; Torres & Hooghiemstra, in prep.). During the late Miocene and early Pliocene, the status of the subpáramo belt is uncertain and perhaps it had not developed into a discrete belt as it did during the Quaternary. Characteristic subpáramo taxa include Asteraceae, Clusiaceae, Ericaceae, Escalloniaceae, Melastomataceae, Myricaceae, Rosaceae, Rubiaceae, and Scrophulariaceae.

The present-day grasspáramo belt extends from ca. 3500 to ca. 4200 m, and annual temperatures average

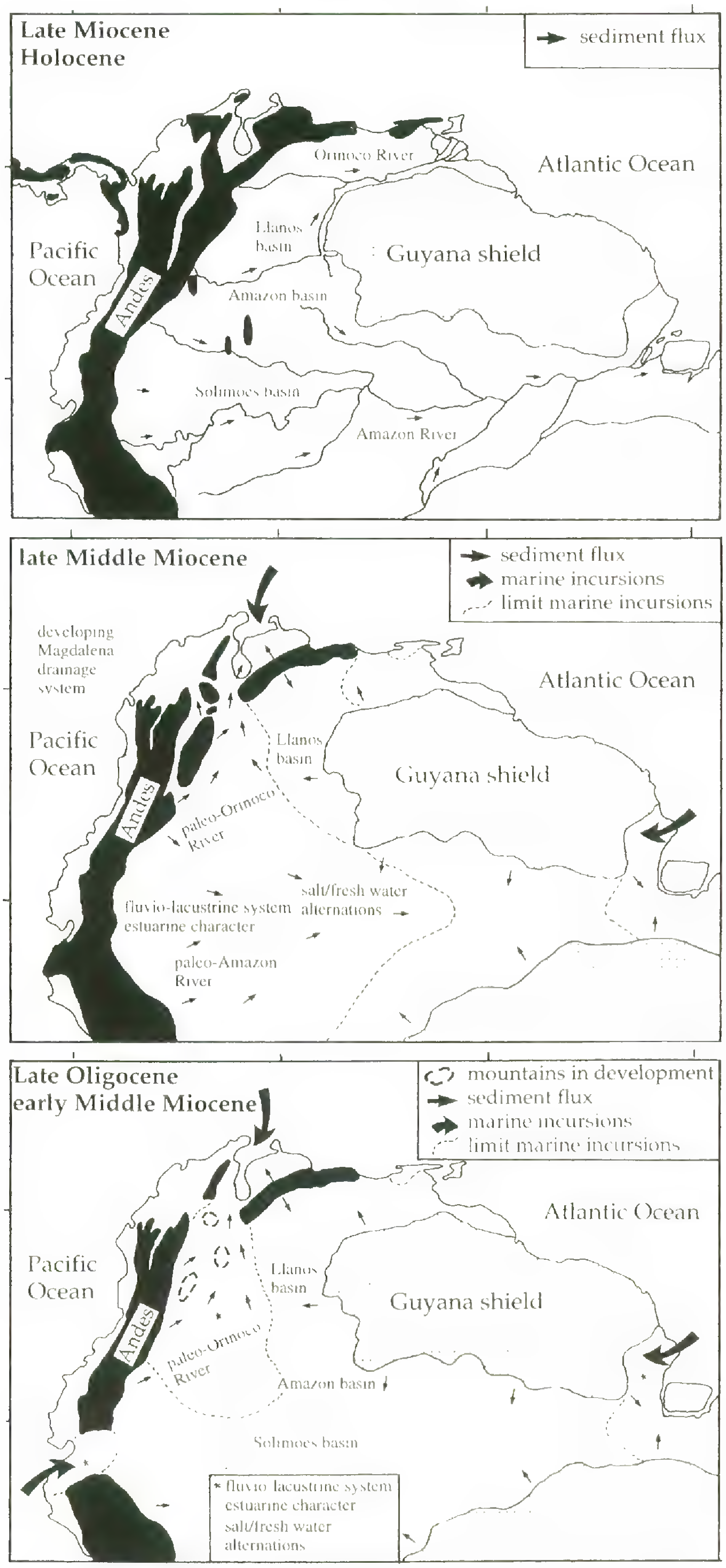

Figure 3. Paleogeographic maps of the (top) late Miocene to Present, (middle) late Middle Miocene, and (bottom) early Middle Miocene of northern South America. The development of the northern Andes, the separation of Chocó and Lower Magdalena rainforest areas from the main area of Amazonian rainforest, and the middle Miocene fluvio-lacustrine system in the present-day central Amazon basin is shown. During periods of high sea level stands, at various places in the present Amazon basin, mangrove vegetation developed under brackish water conditions (the extension of an inland sea is indicated by a dotted line). Between the late Miocene and the Quaternary, the modern Orinoco River system developed from the paleo–Orinoco River and the Amazon River developed as a transcontinental drainage system toward the Atlantic. Reprinted from Hooghiemstra & van der Hammen (1998), with permission from Elsevier. The Hooghiemstra & van der Hammen (1998) figure was created based on Hoorn et al. (1995).

7°C at the lower altitudinal limit to 3°C at the upper altitudinal limit. The vegetation is dominated by graminoid communities associated with stem rosettes of mainly *Espeletia* Mutis ex Bonpl. The most species-rich families in the subpáramo and grasspáramo belts are Asteraceae, Ericaceae, Poaceae, and Polypodiaceae.

The present-day superpáramo belt occurs above the grasspáramo and extends from ca. 4200 m up to the snowline at ca. 4800–5000 m. The annual temperature averages between 3°C and 0°C. The vegetation cover is scarce and patchy due to frequent frosts and unstable soil caused by frost heaving. The vegetation of this belt does not play a relevant role in estimating paleoaltitudes from paleofloras.

Changes of the Paleoenvironmental Setting of Northern South America since the Miocene

The geologic and paleogeographic history of the northern Andes is principally related to the relative motion of continental and oceanic plates. During the late Oligocene of northwest South America, the breaking up of the Farallón Plate in the Nazca and Cocos plates enhanced tectonic activity along the Pacific side of the continent and induced the uplift of the Andes (Wortel & Cloetingh, 1981; Wortel, 1984; Smith, 1985). Plate motions were also responsible for the closing of the Isthmus of Panama during the Pliocene (Keigwin, 1978, 1982; Duque Caro, 1990).

The uplift history of the three Cordilleras in Colombia stretches across the Neogene, but in many places uplift was most important during the period between the Oligocene and the Pliocene, with highest uplift rates during the Pliocene (van der Hammen, 1961; Harrington, 1962; van Houten & Travis, 1968; van der Hamen et al., 1973; Fabre, 1983; Kroonenberg et al., 1990; van der Wiel, 1991; Hoorn et al., 1995). Uplift in some parts of the Western Cordillera occurred during the Miocene. Parts of the Colombian Central Cordillera rose between 22 and 18 million years ago (Ma), whereas parts of the Eastern Cordillera were uplifted between 10 and 4 Ma. The Santander Massif of the Eastern Cordillera was uplifted between 16 and 12 Ma (Kroonenberg et al., 1990). In the Upper Magdalena Valley, the Garzón Massif was uplifted around 12 Ma, which resulted in a fundamental change in the Magdalena River's direction of flow (van Houten & Travis, 1968; van der Wiel, 1991; Guerrero, 1993; Flynn et al., 1994).

Short Recapitulation of Paleobotanical Evidence for Uplift from Sites in Lowland Amazonia

Miocene and Pliocene sediments from exposures in river valleys in Colombian Amazonia showed pollen records that could be dated based on biostratigraphy (Hoorn, 1993; Hoorn et al., 1995). Pollen records from these landlocked sites showed alternations between vegetation characteristic of inland wet forest, open vegetation of coastal plains (with abundant grasses and palms), and mangroves. These environmental changes strongly suggest that during those time intervals marine incursions were able to reach the area that is covered at present by the rainforests of northwest Amazonia. In particular, during periods with high sea-level stands, marine waters penetrated far into the Amazon basin, changing freshwater ecosystems (swamps and inundated forest) into brackish and saltwater ecosystems (mangroves) (Fig. 3). Because ecophysiologic conditions during such changes would have been at extremes, during the Neogene a significant part of Amazonia had to have been repeatedly fully repopulated with a "new" ecosystem.

Uplift of the northern Andes is substantiated by a change in the drainage pattern: during the early Middle Miocene the Guayana Shield was the main source of sediment and the paleo–Orinoco River drained northward into Lake Maracaibo (mainly east-to-west flow direction in Fig. 3). During the late Miocene and Pliocene, the Andes gradually became the main source of sediment that substantiated the process of uplift (mainly a west-to-east flow direction). Closure of the Andean chain by the uplift of the Eastern Cordillera forced the paleo–Orinoco River to migrate eastward to its present-day position.

Paleobotanical Evidence for Uplift from Sites in the High Andes

Fossil pollen and botanical macrofossils were studied in sediments from sections collected at six exposures at ca. 2550 m altitude in the surroundings of the present-day high plain of Bogotá (Fig. 1; Table 1). The fossil taxa were arranged according to their modern altitudinal distribution. Many taxa have altitudinal ranges in common and such ecological groups constitute vegetation belts, which are in fact abstractions. Modern altitudinal ranges are based on studies of the existing vegetation. The assignment of a fossil taxon to a particular ecological group is based on the principal altitudinal range of its present-day relatives. Every time slice shows the relative proportion of the phytogeographic source areas (Fig. 4; Appendix 1). The phytogeographic units are after van der Hammen and Cleef (1986) and Gentry (1986). Additional information on the phytogeographic distribution of the identified fossil taxa was obtained from Kappelle et al. (1992) and Mabberley (1993). The biostratigraphic range of selected pollen and macro-

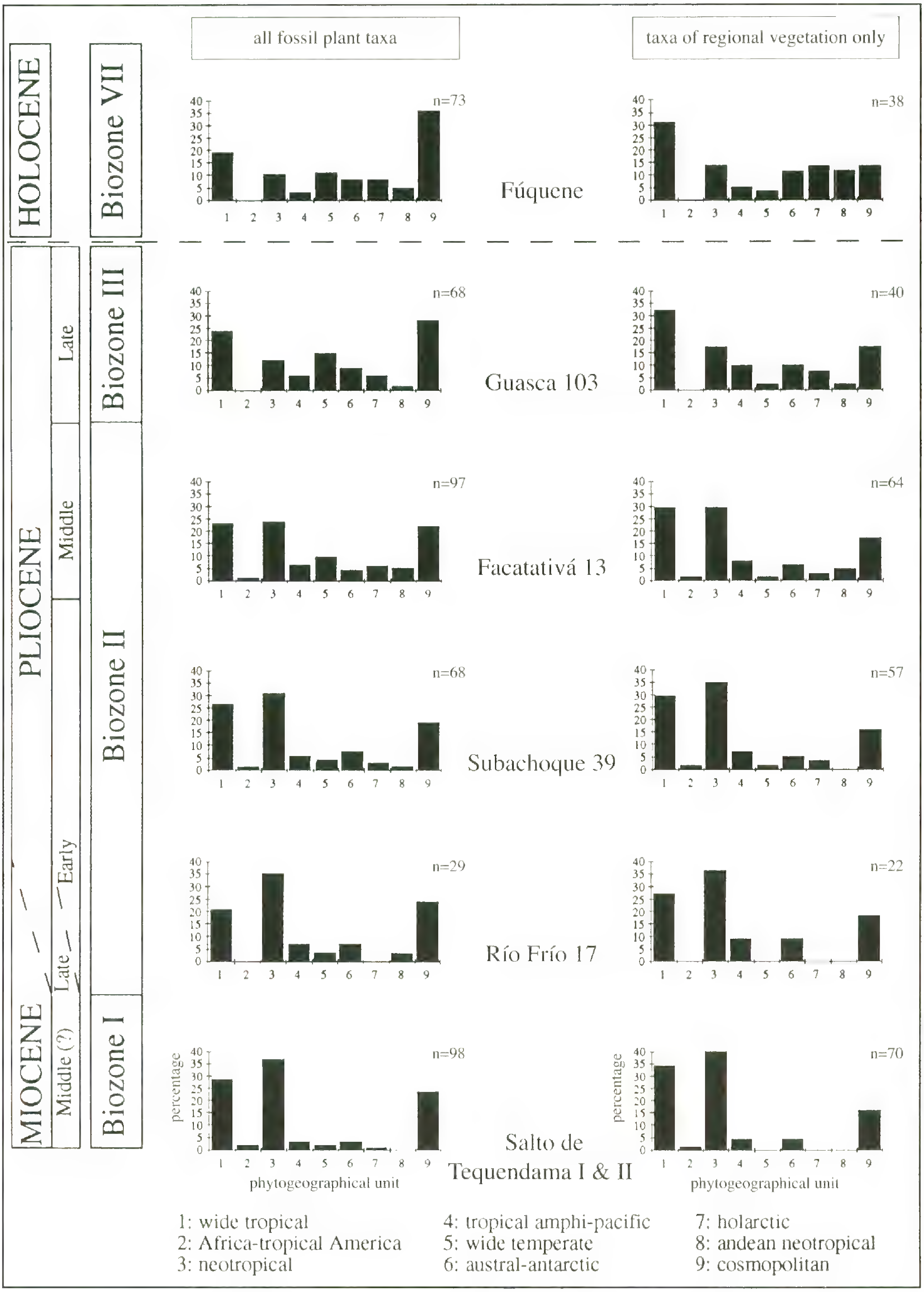

Figure 4. Phytogeographic composition of neogene fossil plant assemblages and paleofloras (only selected taxa are shown) from six sections located at the border of the basin of Bogotá, Colombia. Sections are arranged from the late Miocene (bottom) to the late Pliocene (top) and the present-day composition is shown above the dashed line for comparison. Percentage calculations are based on all identified fossil plant taxa (left), or on a selected group that represents the regional vegetation only. Plant assemblages representative for the Holocene are taken from core Fuquene-2 (van Geel & van der Hammen, 1973).

fossil taxa obtained from these Neogene sediment sequences is presented in Figure 5.

STATISTICAL ANALYSIS OF FOSSIL ASSEMBLAGES

Floristic similarity between fossil assemblages was statistically analyzed (cf. Graham, 1992). Data per ecological group and per section were not normally distributed using 95% confidence intervals (CI). Therefore, the nonparametric Kruskal-Wallis 1-sample test (Sokal & Rohlf, 1981) was chosen to evaluate the degree of dissimilarity between the fossil pollen spectra of sections Salto de Tequendama I and II, Subachoque 39, Facatativá 13, and Guasca 103. Pseudosignificance was expected because 85 individual comparisons were carried out. Pseudosignificance means that if for all tests a 95% CI is used, 5% of random data lie outside the 95% CI and decisions based on conventional levels of significance may be incorrect. Therefore, a more conservative approach was used that lowers the critical probability P for each individual comparison so that the probability of an erroneously rejected null hypothesis in the entire series of tests does not exceed the general critical alpha. The level of confidence for the individual comparisons was calculated as follows:

$$P = 1 - \sqrt[L]{1 - \alpha}$$

(L represents the number of comparisons)

In this case, the level of confidence is 0.0006.

The results of the Kruskal-Wallis tests are shown in Table 2. The tropical lowland taxa assemblages differed significantly in all sections. For the subandean-tropical lowland and Andean-subandean assemblages, site Salto de Tequendama II differed significantly from all other sites. Additionally, for the Andean-subandean assemblage, site Facatativá 13 differed significantly from site Guasca 103. For the Andean assemblage, sites Salto de Tequendama I and II differed significantly from each other as well as from all the other sections. For the subpáramo assemblages, both sites Salto de Tequendama I and Subachoque 39 differed significantly from Facatativá 13 and Guasca 103. The general decrease in floristic affinity between the studied associations is consistent with the decreasing age of these associations. This trend shows that each flora is slightly different in floristic composition from its neighboring floras.

PALEO-PHYTOGEOGRAPHY

The fossil floras from sites in the Bogotá area show a gradual change in plant composition from the late Miocene to late Pliocene. The late Miocene warm tropical lowland taxa are subsequently replaced by taxa with pre-montane and ultimately montane affinities (Figs. 4 and 5). During the late Miocene to late Pliocene, the following trends in the phytogeographic composition of the floras can be observed (Fig. 4): (1) the percentage of wide tropical taxa decreased slightly, (2) neotropical elements decreased markedly, (3) the percentage of cosmopolitan taxa increased; (4) Andean neotropical taxa were present from the middle Pliocene onward, and (5) wide temperate taxa increased significantly. During the late Miocene, Amazonian-centered families made up the majority of the local forest taxa (Fig. 6). Toward the late Pliocene, the proportion of this group gradually decreased. Laurasian elements showed the opposite pattern (van der Hammen & Cleef, 1983), whereas the proportion of Andean-centered taxa remained approximately the same. The calculated similarity values reveal the degree of floristic affinity between the associations (Table 2). The general observation is that calculated values of floristic affinity decline with an increasing difference in age between the floras.

Van der Hammen et al. (1973) used the successive immigration of temperate arboreal taxa, such as *Alnus* Mill., *Hedyosmum* Sw. (not strictly temperate), *Myrica* L., and *Quercus* L., to construct a biostratigraphic framework. He established seven biozones for the sediments in the study area (Table 3) (cf. Kuhry & Helmens, 1990; van der Hammen & Hooghiemstra, 1995; Wijninga, 1996d; van der Hammen & Hooghiemstra, 1997; Torres & Hooghiemstra, in prep.).

UPLIFT OF THE NORTHERN ANDES EVIDENCED BY PALEOBOTANICAL DOCUMENTS FROM LOW AND HIGH ALTITUDES

In the Bogotá area, middle Miocene sediments show dominant warm lowland taxa, whereas late Miocene and Pliocene sediments show increasing proportions of taxa associated with high-elevation vegetation (Table 4; Figs. 4 and 5). This trend in vegetation change is primarily explained in terms of a gradual

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Phytogeographic relationships of the identified taxa are according to van der Hammen & Cleef (1986), Mabberly (1993), and Kappelle et al. (1992). The neotropical and Andean neotropical groups have no taxa in common. (cf. genus name = sp. ined., cf. genus name; aff. genus name = sp. ined., aff. genus name). Modified after Wijninga (1996d).

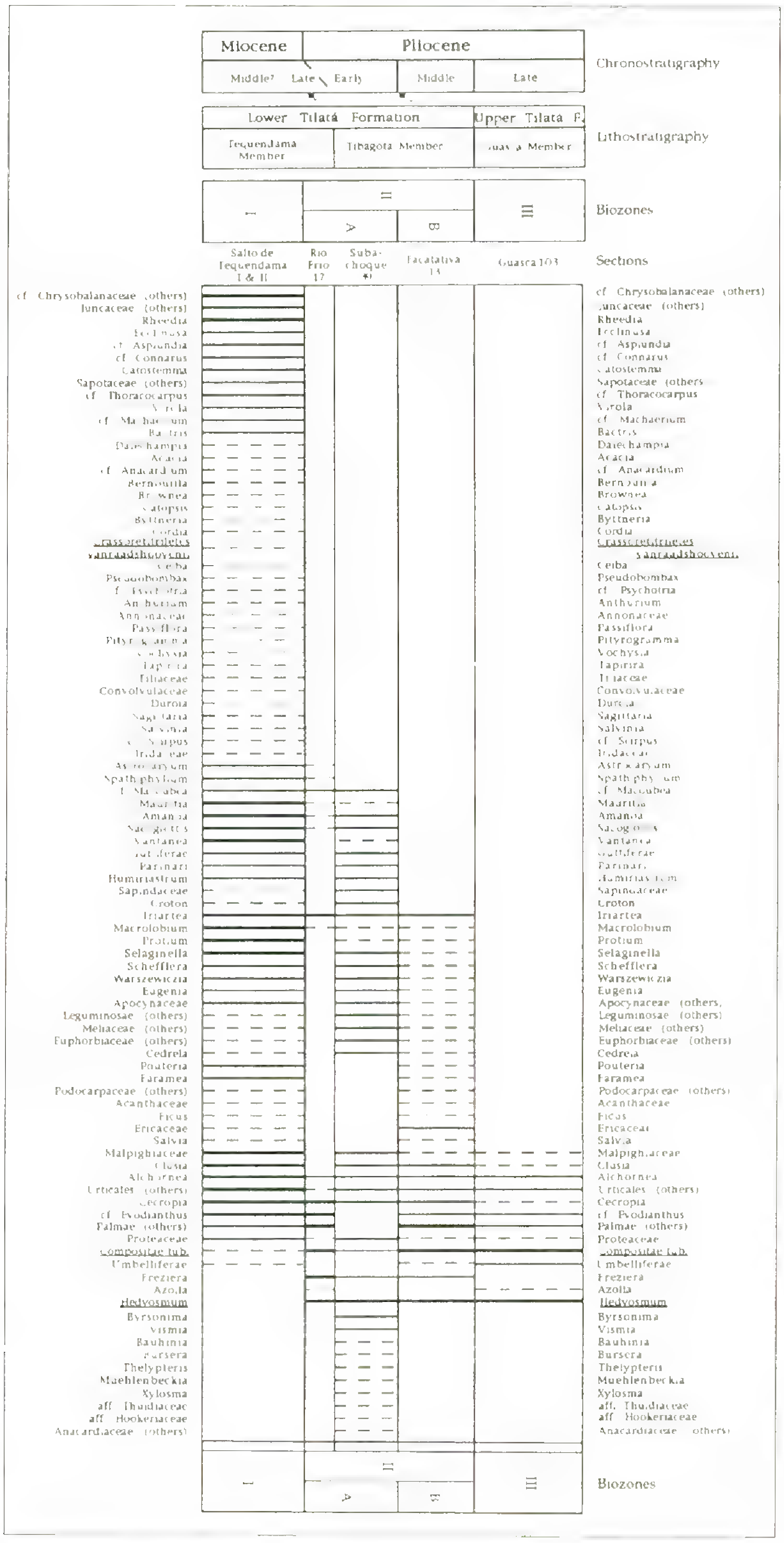

Figure 5. Biostratigraphic range of fossil plant taxa in sections Salto de Tequendama-I and II, Rio Frío-17, Subachoque-39, Facatativá-13, and Guasca-103. Marker taxa for biozones (see Table 3) are underlined. Time control: 1 = 5.3 ± 1 Ma; 2 = 3.7 ± 0.5 Ma. Percentages (thick lines ≥ 10%; thin lines = 10%–1%; dashed lines ≤ 1%) are based on average representation in the pollen or macrofossil diagrams of the respective paleofloras (Wijninga, 1996d).

increase in the elevation of the sedimentary environment and thus reflects a decrease in temperature. However, a temperature decrease is also expected at the transition from the late Pliocene to early Pleistocene, when temperatures decreased on a global scale and the period of Pleistocene ice ages started (e.g., Lohman & Carlson, 1981; Kennett, 1995; Shackleton, 1995). Despite this cooling trend, paleoclimatic studies show that low latitude sea surface temperature showed much less variation, generally in the range of 3°C (Savin et al., 1975; Savin, 1977; Shackleton, 1982; Tiedemann et al., 1994). We therefore assume that Neogene temperatures in montane equatorial South America were maximally 3°C higher than at present. A maximum difference of 3°C corresponds to a 500 m maximum shift of the altitudinal vegetation belts when the modern temperature gradient of 6°C/1000 m is applied (Meyer, 1992; Witte, 1994). This potential temperature shift does not explain the difference between present-day altitude

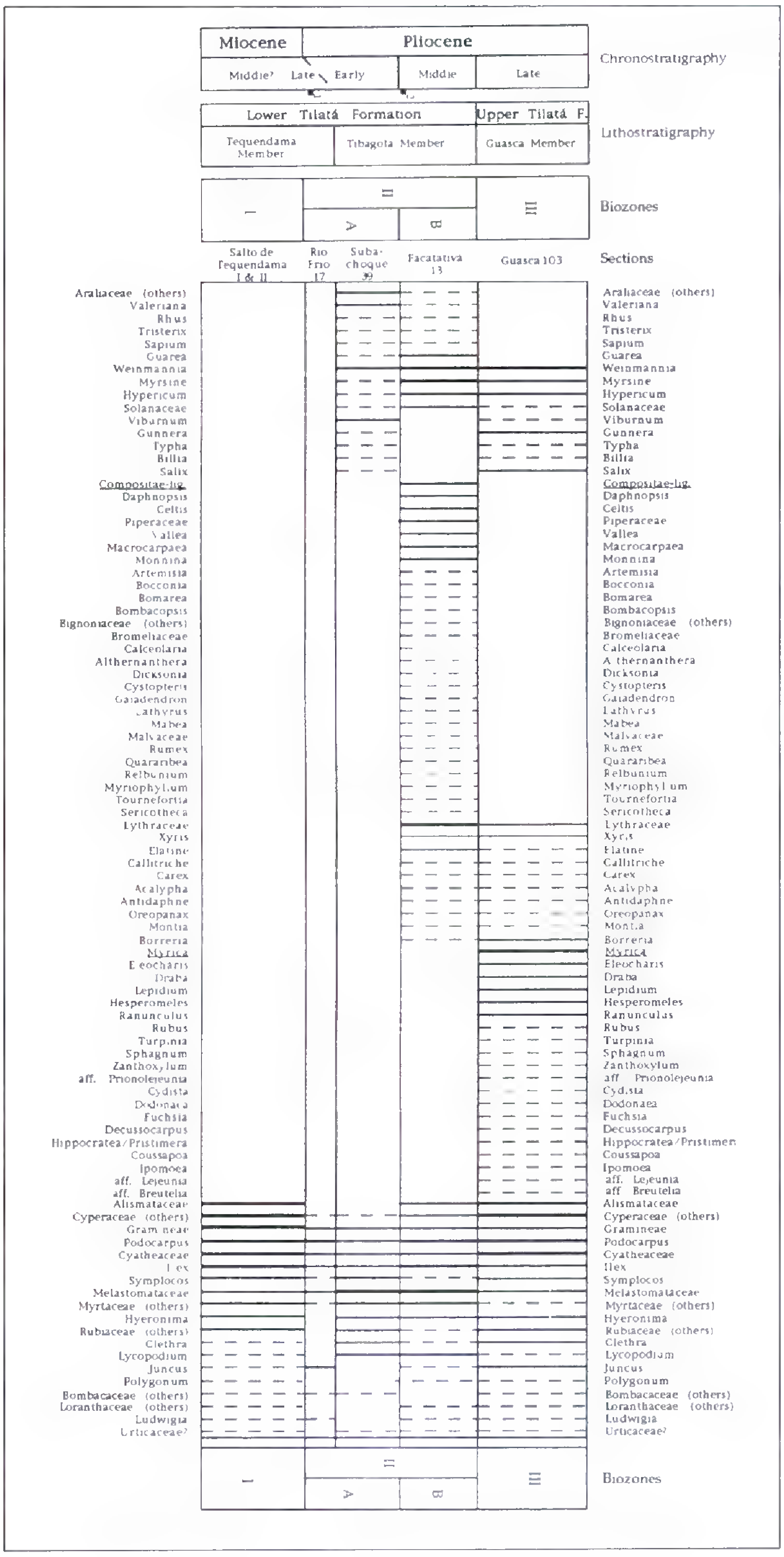

Figure 5. Continued.

and inferred paleoaltitude of sections Salto de Tequendama-I, Salto de Tequendama-II, Río Frío-17, and Subachoque-39. As a consequence, the change in vegetation and the inferred temperature decrease must have been primarily caused by tectonic uplift. When uplift was quantified and plotted against time, the Pliocene was identified as the period with main uplift (Fig. 7).

From the late Miocene onward, a period of approximately 2 to 3 million years elapsed before the area of sedimentation was uplifted to altitudes equivalent to the present-day lowermost limit of the Andean forest belt (2300–2500 m). During this time span, the montane forest evolved. The rate of development in the study area may have been accelerated by the presence of montane forest in other areas. Several middle to late Miocene pollen records from northwestern South America show pollen grains of Podocarpaceae. Podocarpaceae pollen grains may potentially belong to *Nageia* Gaertn., *Podocarpus* L'Hér. ex Pers., *Prumnopitys* Phil., and/or *Retrophyllum* C. N. Page (Lorente, 1986; Hoorn, 1993, 1994a, 1994b; Behling, 1996; Wijninga, 1996a). In the northern Andes, representatives of the Podocarpaceae occur mainly as single trees or as groups of trees in the Andean upper montane rain forest; at

Table 2. Results of the Kruskal-Wallis 1-sample test applied to the floral assemblages of five sections from the area of Bogotá: Salto de Tequendama I and II, Subachoque 39, Facatativá 13, and Guasca 103; sections are dated from middle Miocene to late Pliocene, respectively. Individual significance level, $P = 0.0006$; global significance level, $\alpha = 0.05$. Significant scores are in bold; — no data available. Results show floristic dissimilarity between five sections for five different ecological assemblages, ranging from tropical lowland to subpáramo.

	S. de Tequend. II	Subachoque 39	Facatativá 13	Guasca 103
Tropical lowland assemblages				
S. de Tequendama I	**0.0000**	**0.0000**	**0.0000**	**0.0000**
S. de Tequendama II		**0.0000**	**0.0000**	**0.0000**
Subachoque 39			**0.0000**	**0.0000**
Facatativá 13				**0.0000**
Subandean-tropical lowland assemblages				
S. de Tequendama I	**0.0000**	0.0104	0.0051	0.8114
S. de Tequendama II		**0.0002**	**0.0000**	**0.0000**
Subachoque 39			0.0008	0.3717
Facatativá 13				0.1524
Andean-subandean assemblages				
S. de Tequendama I	**0.0000**	0.3207	0.0018	0.0602
S. de Tequendama II		**0.0000**	**0.0000**	**0.0000**
Subachoque 39			0.2072	0.0148
Facatativá 13				**0.0000**
Andean assemblages				
S. de Tequendama I	**0.0000**	**0.0000**	**0.0000**	**0.0000**
S. de Tequendama II		**0.0000**	**0.0000**	**0.0000**
Subachoque 39			0.5002	0.3100
Facatativá 13				0.1646
Subpáramo assemblages				
S. de Tequendama I	—	0.5949	**0.0000**	**0.0000**
S. de Tequendama II		—	—	
Subachoque 39			**0.0002**	**0.0003**
Facatativá 13				0.3703

present Podocapaceae have been removed in most forests to produce timber. Stands of *Podocarpus*-dominated forest have been reported from, among others, the Mérida Andes ca. 2500 m (Vareschi, 1980), the Serranía de Perija between 3300 and 3500 m (J. O. Rangel, personal communication), and near Loja, Ecuador, in the Podocarpus National Park. The lowermost part of the Funza-2 pollen record (Torres, 2006; Torres & Hooghiemstra, in prep.) shows that before 2 Ma Podocarpaceae were more abundant in equatorial montane forests. Patches of modern Podocarpaceae-dominated forest may represent the last relicts of the original montane forest. Podocarpaceae-dominated forest was more common before the immigration of arboreal elements from northern and southern latitudes and before warm neotropical taxa adapted to cool and cold conditions. The late Miocene evidence of Podocarpaceae pollen grains points to the existence of montane forest, although it has to be stressed that only a few modern species of Podocarpaceae occur as rare trees scattered over the lowlands of Amazonia and in the Chocó biogeographic region along the Pacific coast of Colombia (Rangel, 2004). According to W³ TROPICOS (2006), *Podocarpus magnifolius* J. Buchholz & N. E. Gray is recorded from Panama to the Bolivian Amazon and in Colombia and Venezuela up to ca. 2000 m in the lower montane rain forest belt.

Earlier uplifted areas in the environs of the basin of Bogotá are the Garzon, Quentame, and Santander massifs, and the Central Cordillera. All of these may have been populated by some type of early Andean forest and may have been the sources for a newly developing flora and vegetation in the newly uplifted mountain areas. Taxa already adapted to cool climatic conditions may have accelerated the formation of monodominant upper montane forest in the area under study.

Forty taxa of the modern páramo belt have been recorded in the fossil assemblages. Among these taxa are *Xyris* L., *Miconia* Ruiz & Pav., *Eleocharis* R. Br., and *Scirpus* L., which are shared with lowland savanna flora (Cleef et al., 1993). *Xyris* probably originated

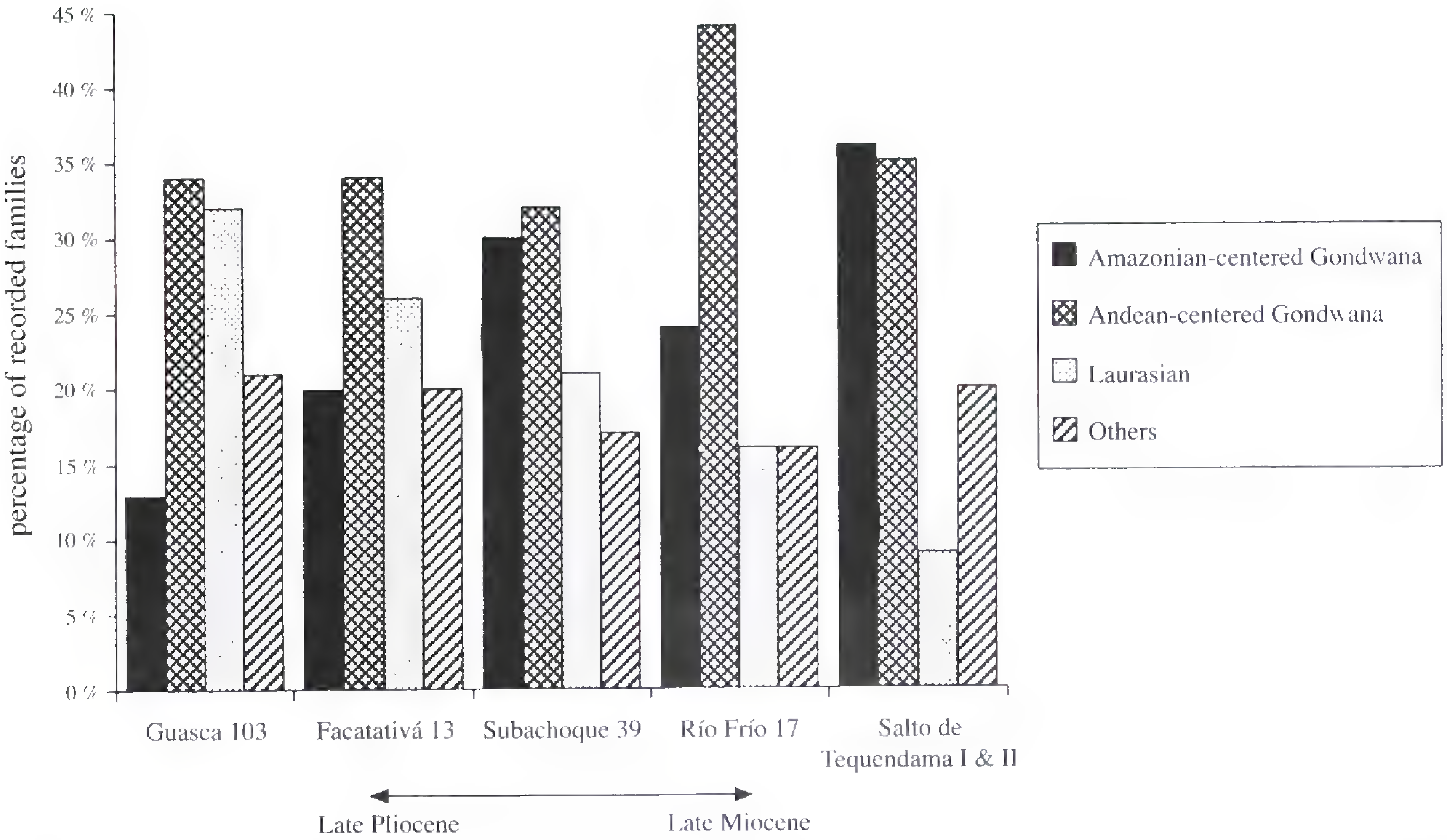

Figure 6. Relative contribution of Amazonian-centered Gondwanan, Andean-centered Gondwanan, and Laurasian families to the composition of the fossil plant assemblages of sections Salto de Tequendama-I and II (Middle Miocene), Rio Frío (late Miocene to early Pliocene), Subachoque-39 (early Pliocene), Facatativá-13 (middle Pliocene), and Guasca-103 (late Pliocene). Modified after Wijninga (1996d).

from the open warm tropical lowlands and underwent gradual adaptation to cool climatic conditions during the uplift of the Eastern Cordillera. Finally, *Xyris* became part of the páramo vegetation. However, plant macroremains, of *Xyris* in particular (Wijninga, 1996b), indicate swamps are present in the different forest belts. This does not exclude their former occurrence in exposed mountain savannas as suggested by Cleef et al. (1993). *Miconia* is mainly an important component of the understory of (successional) lowland and montane rain forest. Wijninga (1996b) identified remains of Pliocene seeds to the taxonomic levels of the Miconieae and *Miconia*. It is difficult to assess whether species of *Eleocharis* and *Scirpus* in the northern Andes are from tropical or temperate origin.

In addition, other characteristic taxa of modern subpáramo and grasspáramo, such as *Acaena* Mutis ex L., *Polylepis* Ruiz & Pav., *Aragoa* H.B.K., *Arcytophyllum* Willd. ex Schult., *Bartsia* L., Caryophyllaceae, *Clinopodium* L. (= *Satureja*), *Eryngium* L., *Plantago* L., and *Puya* Molina, were absent during the Pliocene. Van der Hammen and Cleef (1986) postulated the presence of a hypothetical "prepáramo" (i.e., an open type of vegetation occurring locally on exposed hilltops before the final uplift of the Eastern Cordillera) and also a "proto-páramo" (i.e., early páramo vegetation with characteristic páramo taxa, but still poor in species). The suggested local presence of late Miocene open vegetation on hilltops may represent pre-páramo vegetation (Biozone I; Grubb, 1971; Wijninga, 1996a). The fossil

Table 3. Main characteristics of northern Andean Biozones I to VII (after van der Hammen et al., 1973). Biozones IV to VII also follow from cluster analysis of the pollen assemblages of the Funza-2 record (Torres, 2006; Torres & Hooghiemstra, in prep.).

Biozone	Age	First appearance date/Taxon dominance
Biozone I	middle to late Miocene	abundant *Mauritia*, *Iriartea*, Bombacaceae
Biozone II	early Pliocene	start of the record of *Hedyosmum*
Biozone III	late Miocene	start of the record of *Myrica*
Biozone IV	middle Pliocene	abundant *Borreria*
Biozone V	late Pliocene	abundant *Juglans* and *Plantago*
Biozone VI	early Pleistocene	start of the record of *Alnus*
Biozone VII	middle Pleistocene	start of the record of *Quercus*

Table 4. Recovered pollen taxa in six sections located at the border of the basin of Bogotá, arranged from the late Miocene (left) to the late Pliocene (right). Taxa are arranged based on modern ecological and altitudinal affinities. Data from Wijninga (1996d).

	Salto de Tequendama I	Salto de Tequendama II	Río Frío 17	Subachoque 39	Facatativá 13	Guasca 103
Grasspáramo taxa (3500–4200 m)	Poaceae[1]	Poaceae[1]	Poaceae[1]	Poaceae[1]	Poaceae[1]	Poaceae[1]
Subpáramo taxa (3200–3500 m)/ montane open vegetation taxa	Asteraceae-tubuliflorae Asteraceae-liguliflorae Ericaceae		Ericaceae[2]	Asteraceae-tub.[1] *Hypericum*	Asteraceae-tub.[1] *Hypericum*	Asteraceae-tub.[1] *Hypericum*
Andean forest belt taxa (2300–3200 m)	*Clethra* *Hedyosmum* *Symplocos*	*Hedyosmum*	*Hedyosmum* *Symplocos*	*Clethra*-type *Eugenia*-type *Hedyosmum* *Ilex* *Myrsine* *Symplocos* *Viburnum* *Weinmannia* *Xylosma*	*Bocconia*[2] *Clethra*[2] *Gaiadendron* *Hedyosmum* *Ilex* *Macrocarpea* *Myrica*[2] *Myrsine* *Oreopanax*[2] *Sericotheca*[2] *Symplocos* *Vallea* *Weinmannia*	*Clethra*-type *Eugenia* *Hedyosmum* *Hesperomeles*-type *Ilex* *Myrica* *Myrsine* *Oreopanax* *Symplocos*[1] *Viburnum* *Weinmania*
Andean forest belt-subandean forest belt taxa (1000–3300 m)	*Clusia* Clusiacae (others) Melastomataceae Myrtaceae (others) *Podocarpus* Proteaceae	Melastomataceae Myrtaceae (others) *Podocarpus* Proteacae	Melastomataceae Myrtaceae (others) Podocarpus Proteacae	Araliaceae *Billia* Clusia-type Clusiaceae Melastomataceae Myrtaceae *Podocarpus* Proteaceae *Salix* Solanaceae	Araliaceae[2] *Celtis* *Clusia*-type *Daphnopsis* Euphorbiaceae (others) Melastomataceae[1] *Monnina* Myrtaceae (incl. *Eugenia*) Piperaceae *Podocarpus*[1] Proteaceae Solanaceae	*Billia* *Clusia*-type Melastomataceae[1] Myrtaceae (others) *Podocarpus* Proteaceae Solanaceae

Table 4. Continued.

	Salto de Tequendama I	Salto de Tequendama II	Río Frío 17	Subachoque 39	Facatativá 13	Guasca 103
Subandean forest belt-tropical lowland taxa (0–2300 m)	*Alchornea*	*Alchornea*	*Alchornea*	*Alchornea*	*Acalypha*	*Acalypha*
	Apocynaceae (others)	Apocynaceae (others)	Arecaceae (others)	Apocynaceae (others)	*Alchornea*	*Alchornea*
	Arecaceae (others)	Arecaceae	Urticales	*Bauhinia*	*Apocynaceae*	Arecaceae
	Burseraceae/Sapotaceae	*Cordia*[2]		*Cecropia*	*Arecaceae*	*Cecropia*[2]
	Cecropia	*Faramea*		*Cedrela*-type	*Cecropia*[1]	*Hyeronima*
	Cedrela	Malpighiaceae		Euphorbiaceae (others)	*Cedrela*	Malpighiaceae
	Cordia[2]	cf. Rubiaceae		*Guarea*-type	*Faramea*	Meliaceae
	Croton	*Schefflera*[2]		*Hyeronima*	*Ficus*[2]	Rubiaceae
	cf. Euphorbiaceae	Urticales (others)		Fabaceae (others)	*Guarea*	*Salix*
	Fabaceae (others)			Malpighiaceae	*Hyeronima*	Urticales (others)
	Fabaceae			Meliacae (others)	*Fabaceae (others)*	
	Faramea			*Paraprotium*-type	*Mabea*	
	Hyeronima			*Rhus*	*Malpighiaceae*[2]	
	Malpighiaceae			Rubiaceae (others)	*Meliaceae*	
	Meliacae (others)			Sapindaceae	*Rhus*	
	Rubiaceae (others)			*Sapium*	*Rubiaceae-type*	
	Sapindaceae			*Schefflera*	*Rubiaceae*	
	Schefflera			Urticales (others)	*Sapium*	
	Urticales (others)			*Vismia*	*Tournefortia*	
	Warszewiczia			*Warszewiczia*	*Urticales (others)*	
				Zanthoxylum[2]	*Warszewiczia*	

Table 4. Continued.

	Salto de Tequendama I	Salto de Tequendama II	Río Frío 17	Subachoque 39	Facatativá 13	Guasca 103
Tropical low land taxa (0–1000 m)	*Acacia*	*Amanoa*	*Amanoa*	*Amanoa*	Bignoniaceae	Bombacaceae
	Amanoa	Annonaceae[2]	*Astrocaryum*	Anacardiaceae[2]	*Bombacopsis*	
	Annonaceae	*Astrocaryum*[2]	Bombacaceae	Bombacaceae	*Iriartea*	
	Astrocaryum	*Bactris*	*Ilex*	*Bursera*[2]	*Macrolobium*[2]	
	Bernoullia	Bombacaceae (others)	*Iriartea*	*Byrsonima*	*Pouteria*[2]	
	Bombacaceae (others)	*Byttneria*	cf. *Macoubea*	*Humiriastrum*	*Protium*[2]	
	Brownea	*Catostemma*	*Macrolobium*	*Iriartea*	*Quararibea*	
	Byttneria	*Ceiba*	*Mauritia*	cf. *Macoubea*	*Trichantera/Bravaisa*[2]	
	Catostemma	*Clusia*[2]	*Spatiphyllum*	*Macrolobium*		
	Ceiba	*Eugenia*[2]		*Mauritia*		
	cf. Chrysobalanaceae	*Ficus*		cf. *Sacoglottis*		
	cf. *Connarus*	*Humiriastrum*				
	Dalechampia	*Ilex*				
	Duroia[2]	*Iriartea*				
	Ecclinusa	cf. *Machaerium*				
	Eugenia	cf. *Macoubea*				
	Ficus	*Macrolobium*				
	Humiriastrum	*Mauritia*				
	Ilex	*Pouteria*				
	Iriartea	*Protium*[2]				
	cf. *Machaerium*	cf. *Psychotria*				
	Macrolobium	*Spathiphyllum*				
	Mauritia	*Tapiria*				
	Pouteria	Tiliaceae[2]				
	Protium	*Virola*[2]				
	Pseudobombax	*Warszewiczia*[2]				
	Rheedia					
	Sapotaceae (others)					
	Spathiphyllum					
	Tapirira					
	Virola					
	Vochysia[2]					

[1] Poaceae may reflect mainly local vegetation (and are excluded from the percentage calculations and statistical analysis elsewhere in this paper).
[2] Taxa with low frequency (omitted from the statistical analysis elsewhere in this paper).

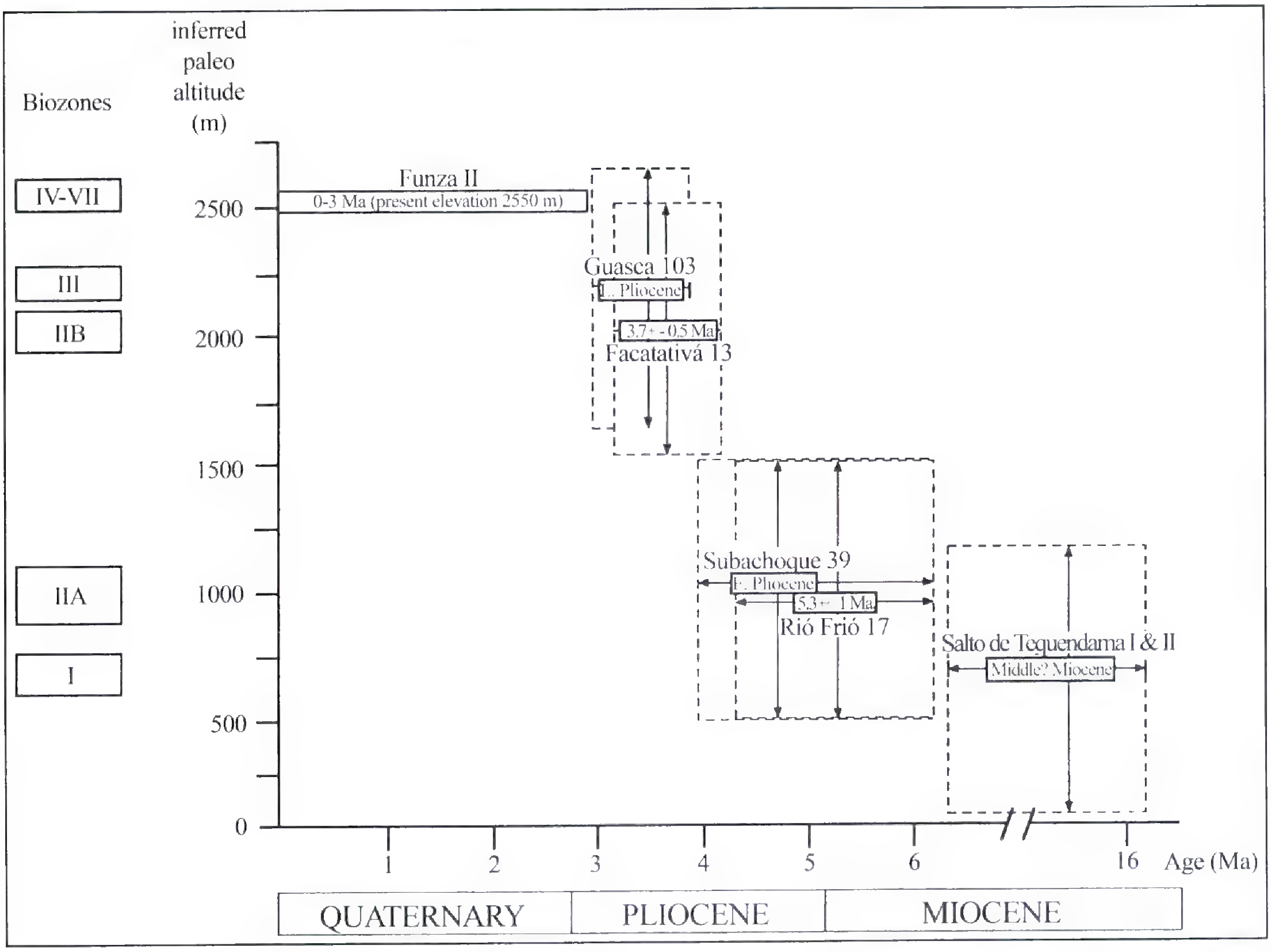

Figure 7. Main chronological, biostratigraphic, paleoenvironmental, and paleoaltitudinal properties of the five sections from exposures in the outer valleys of the basin of Bogotá, Colombia, representing the middle Miocene to late Pliocene. Elevation of past depositional environments was estimated by comparing paleofloras with present-day equivalents. Sediments were dated by fission track dating of intercalated volcanic ashes. Sections make a diagonal in this age vs. paleo-altitude diagram, indicating uplift of the Eastern Cordillera during the late Miocene and Pliocene. Vertical arrows correspond to an estimated uncertainty of ca. 3°C. The basin of Bogotá itself started to accumulate sediments when the Andes had reached its present-day elevation, which is reflected by the position of Funza-2 pollen spectra. For Biozones see Table 3. Modified after Wijninga (1996d).

assemblages discussed here (Biozone II to Biozone III) do not show evidence for the existence of proto-páramo vegetation. The first possible record of proto-páramo or páramo-like vegetation is from the late Pliocene (Biozone IV; van der Hammen et al., 1973; Helmens & van der Hammen, 1994; Torres & Hooghiemstra, in prep.).

Despite the fact that the uplift of the Eastern Cordillera ceased by the end of the Pliocene, the floristic composition of the Andean forest was subject to change up to the late Quaternary. Throughout this period, forest types without modern analogues developed, existed for a while, and became further modified by new migrants, such as *Alnus* and *Quercus* (van der Hammen & González, 1964; van der Hammen et al., 1973; van der Hammen, 1974; Hooghiemstra, 1984; Hooghiemstra & Cleef, 1995; van't Veer & Hooghiemstra, 2000). The latest chronology of the sediments of the basin of Bogotá comes from astronomical tuning of the arboreal pollen record, and consequently first appearance dates from van't Veer and Hooghiemstra (2000) have been corrected (Torres, 2006; Torres & Hooghiemstra, in prep.; Torres et al., in prep.).

Toward the late Pliocene, the fossil floras show at the family level an enrichment of taxa with a Laurasian affinity, and taxa with an Amazonian-centered affinity became less important. These trends are in accordance with the change from tropical lowland environments to Andean forest conditions. The slight decrease in the percentage of Andean-centered elements could be caused by the fact that in the montane forest these families represent predominantly epiphytic and understory shrubs (Gentry, 1982), which are generally underrepresented in the fossil record.

The Dynamic Páramo Archipelago and Speciation

During the Quaternary the upper forest line migrated between ca. 2000 m (during the coldest

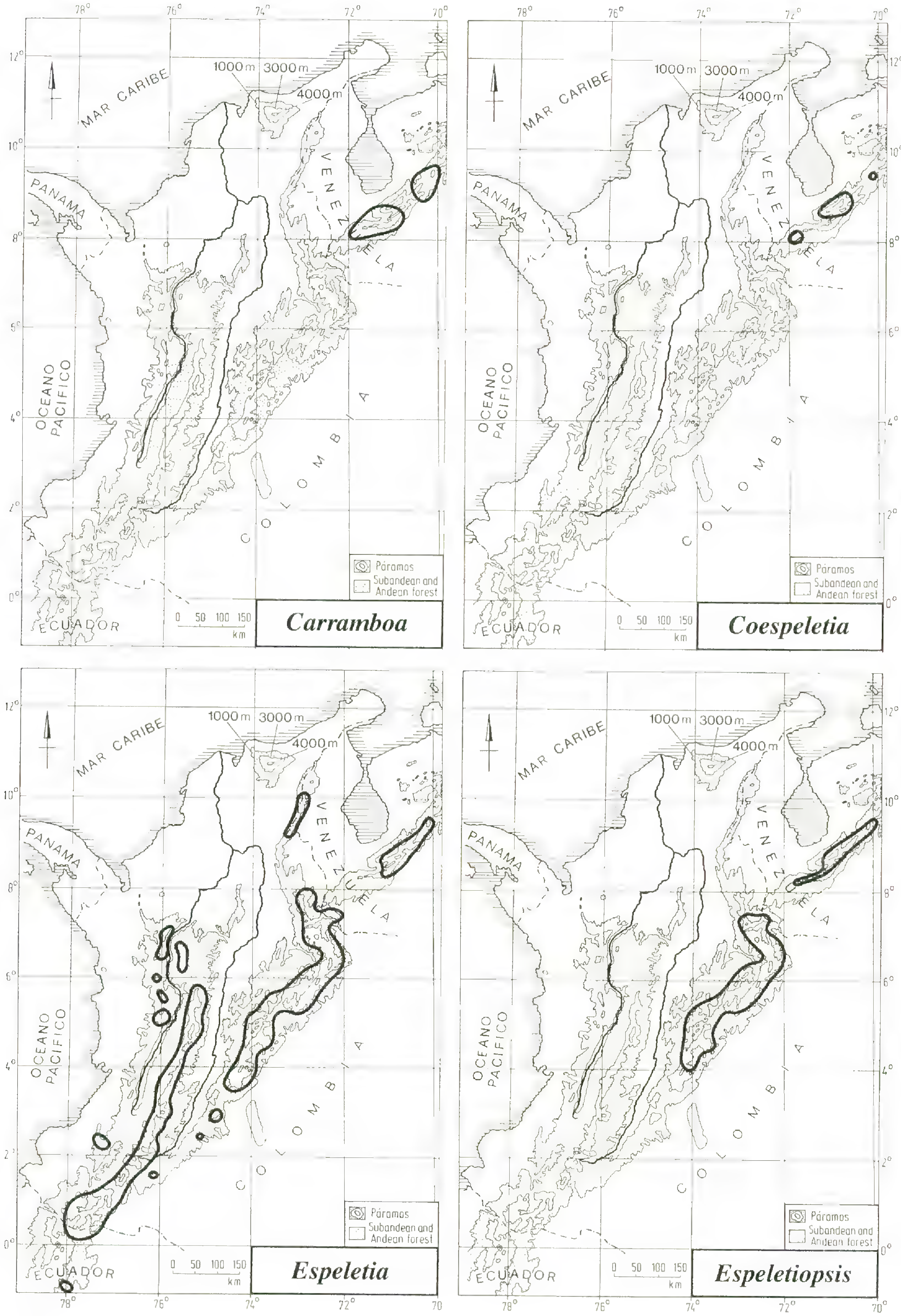

Figure 8. Maps showing the distribution of eight genera belonging to the Espeletiinae (Asteraceae). All genera are endemic to the northern Andes, and many distribution areas coincide with the geologically youngest parts of the Andes.

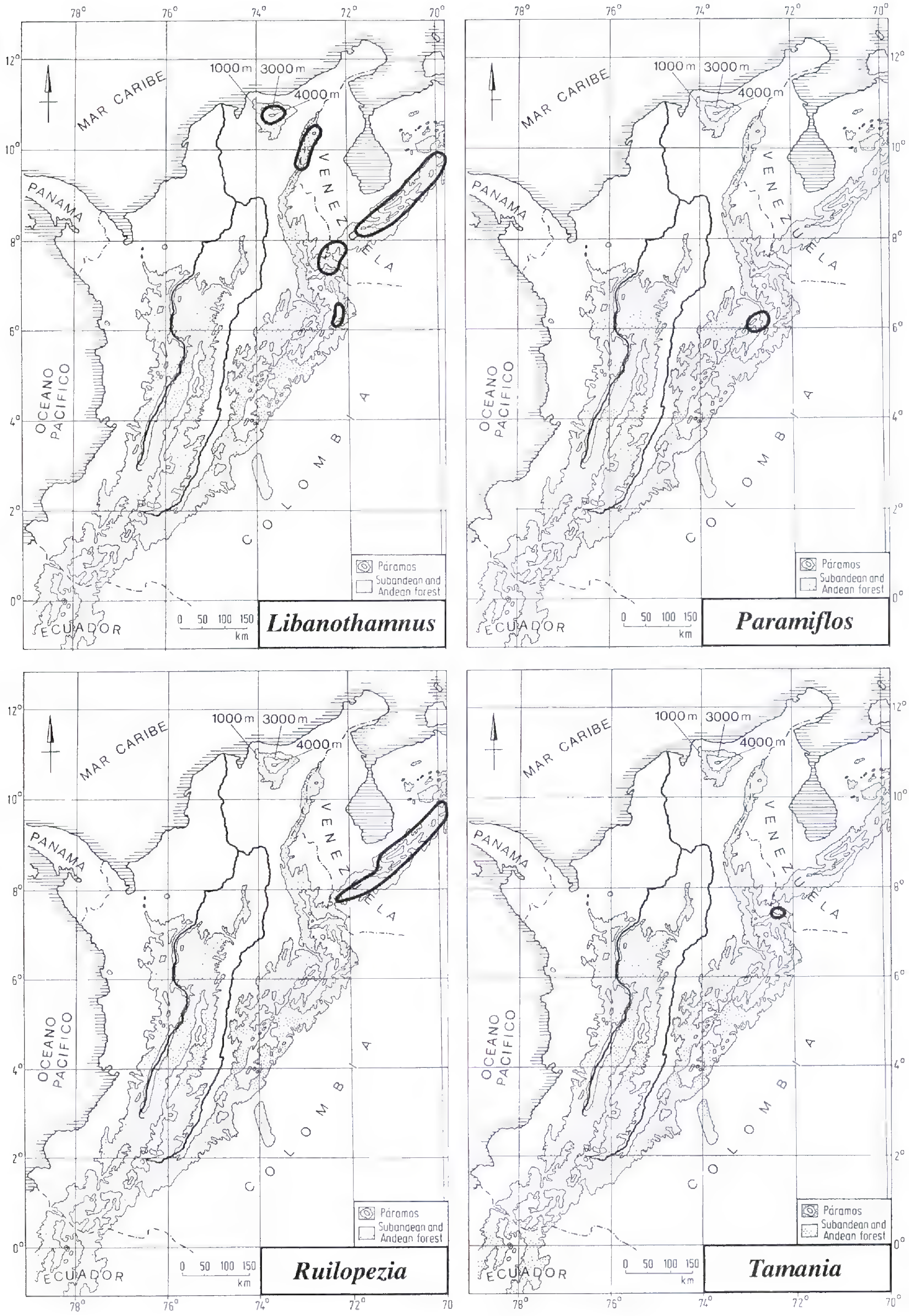

Figure 8. Continued.

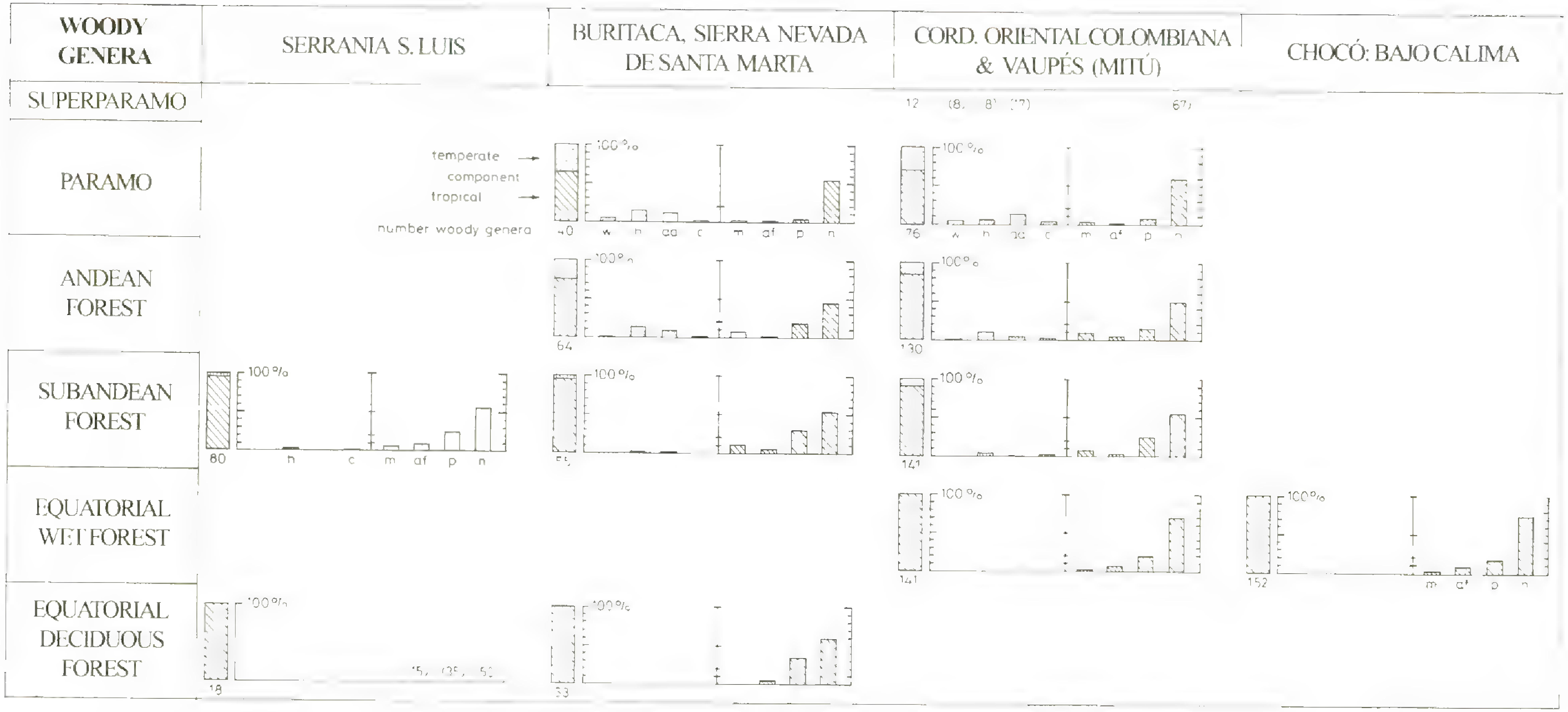

Figure 9. Representation of geographic elements of woody genera for six different vegetation belts in northern Andean and adjacent lowland vegetation showing the adaptation of neotropical lowland taxa to cool climatic conditions. Data are specified (from left to right) for the Serrania San Luis (Venezuela) (subandean forest (1200–1500 m) and deciduous forest (700–1200 m) after Steyermark (1975)); the Buritaca area in the Sierra Nevada de Santa Marta (páramo (> 3300 m), Andean forest (2500–3300 m), and subandean forest (1300–2500 m) based on Rangel & Jaramillo (1984)); Barranquilla (dry deciduous lowland forest after Dugant (1941)); Vaupés (lowland rainforest of Amazonia near Mitú-Caruru, after Cuatrecasas (1958)); the Eastern Cordillera of Colombia (Andean forests after van der Hammen & Jaramillo (unpublished data), and páramos after Cleef (1979) with corrections); and Chocó (Bajo Calima) (lowland rainforest of Amazonia near Trojita-La Brea, after Cuatrecasas (1958)). The bar to the left of each graph shows the number of woody genera and the proportion of tropical and temperate taxa. Phytogeographic elements: n = neotropical; p = pantropical; af = African and American; m = southeast Asian and American; c = cosmopolitan; aa = Austral-Antarctic; h = Holarctic; w = wide temperate. Numbers in parentheses show representation (percentages) of floral elements based on a low total number of genera. After Cleef, unpublished data.

episodes of glacials) and ca. 3200–3400 m (during the warmest episodes in interglacials) (e.g., van der Hammen, 1974; Hooghiemstra, 1984; van't Veer & Hooghiemstra, 2000; Wille et al., 2001). As a consequence, the area covered with páramo vegetation has changed accordingly, from many small areas at mountaintops during interglacial periods (high position of the upper forest line) to large united areas during glacial periods (low position of the upper forest line) (van der Hammen, 1974; van der Hammen & Cleef, 1986). The series of ice ages during the Quaternary caused these altitudinal migrations to repeat many times, potentially leading to a relevant mechanism of speciation.

Cuatrecasas (1979) studied species diversity and distribution areas of the Espeletiinae (Asteraceae). He identified the northern part of the Eastern Cordillera of Colombia (i.e., the Cocuy area and the area north of Chicamocha Valley up to the Mérida Andes) as the area with the highest number of species. The Espeletiinae include the genera *Carramboa* Cuatrec., *Coespeletia* Cuatrec., *Espeletia* Mutis ex Bonpl., *Espeletiopsis* Cuatrec., *Libanothamnus* Ernst, *Paramiflos* Cuatrec., *Ruilopezia* Cuatrec., and *Tamania* Cuatrec. The genera *Espeletia* and *Espeletiopsis* are exclusive to the Colombian and Venezuelan parts of this area, while the genus *Coespeletia* is exclusive to the Venezuelan part of this area. These genera comprise morphologically and ecologically diverse plants and occur in the altitudinal range between 2500 and 4500 m (Rauscher, 2002). Figure 8 shows distribution maps of the genera of the Espeletiinae and shows this area as the center of origin of this taxonomic group (cf. van der Hammen & Cleef, 1986). Notably, the area of highest diversity among Espeletiinae is also the place where the northern Andes is youngest, geologically speaking. According to Luteyn (1999), Colombia has ca. 45 species of *Espeletia* and ca. 16 species of *Espeletiopsis*. Venezuela has ca. 15 species of *Espeletia*, ca. 5 species of *Espeletiopsis*, and ca. 6 species of the genus *Coespeletia*. Many of these taxa show a very limited distribution area and sometimes are restricted to a single mountaintop (Luteyn, 1999). On the Quaternary time scale, the Holocene is among the periods during which distribution areas have a minimal surface. Placing the recent anthropogenic pressure on the páramo ecosystem in this context, many species are relatively close to extinction.

The Andean uplift played a major role in the development and distribution of the present-day northern Andean flora. Numerous neotropical lowland taxa adapted to the cool climatic conditions at high elevation. Additionally, the Andes served as a route for temperate taxa to migrate from temperate latitudes to cool tropical montane areas. The result of these two phenomena can be seen in the present-day composition of the flora of the Colombian montane forest and páramo. Figure 9 supports this view as it shows the representation of geographic elements of woody genera for five different main vegetation belts in northern Andean and adjacent lowland vegetation. At high elevations, temperate taxa are abundant while at low elevations neotropical and pantropical taxa are abundant. A minority of Holarctic elements appear below the Andean forest belt.

Discussion and Synthesis

During the late Miocene (Biozone I), the area of the present-day Bogotá basin was a lowland riverine environment (ca. 700 m elevation) dominated by tropical lowland taxa which, at present, are found in the modern várzea forest of the Amazon basin. This "pre-uplift" vegetation principally consisted of taxa with a wide tropical or neotropical origin (e.g., Bombacaceae, Cyclanthaceae, Humiriaceae, *Iriartea* Ruiz & Pav., *Mauritia* L. f., Melastomataceae, and *Parinari* Aubl.). Amazonian and Andean-centered families were predominant. Trees of Podocarpaceae, accompanied by *Symplocos* Jacq., *Clethra* L., and probably *Weinmannia* L., apparently were constituents of the Neogene montane forests found on elevated areas near the study area.

By the late Miocene to early Pliocene (Biozone IIA), the proportion of tropical lowland taxa had decreased from 75% (Biozone I) to ca. 60%. The share of taxa from present-day Andean and subandean vegetation belts increased from 5% (Biozone I) to 20%. During Biozone IIA, the proportion of Laurasian families increased from 10% to ca. 23%. These changes in the floral composition show a transition from tropical lowland to subandean forest and suggest the local uplift of the Eastern Cordillera to ca. 1000 m elevation. Some tropical lowland taxa, such as Humiriaceae, *Mauritia*, and *Parinari*, persisted in areas, such as valleys, that were still below 1000 m elevation. A number of present-day montane taxa, including those of neotropical origin (e.g., *Billia* Peyr., *Freziera* Sw. ex Willd., *Myrsine* L., and *Xylosma* G. Forst.), appeared for the first time in the study area, indicating a more diverse subandean and apparently Andean forest.

During the middle Pliocene (Biozone IIB), the floral composition was still characterized by a dominance of taxa with a tropical affinity, whereas only 25% of the taxa had either tropical amphipacific, wide temperate, Austral-Antarctic, Holarctic, or Andean neotropical affinities. Based on the affinity of their taxa, the floras of Biozones IIA and IIB are very similar. Alternatively, a comparison between floral composition has been

made on the basis of plant affinity to present-day altitudinal vegetation belts. Around 50%–60% of the Pliocene taxa also belong to present-day subandean and Andean vegetation belts. In contrast to a comparison based on phytogeographic composition, the difference in floral composition between Biozones IIA and IIB is now significant. The characteristics of the vegetation suggest that the area had reached an altitude of ca. 2000 m. Prominent taxa in the montane forest included trees of Podocarpaceae, as well as *Hedyosmum* Sw., *Ilex* L., *Myrsine* L., and *Weinmannia* L. Taxa that first appeared in the studied sequence are *Alternanthera* Forssk., Asteraceae (Liguliflorae), *Bocconia* Plum ex L., *Borreria* G. May, *Calceolaria* L., *Callitriche* L., *Daphnopsis* Mart., *Gaiadendron* G. Don., *Elatine* L., *Montia* L., *Myrica* L., *Quararibea* Aubl., *Sericotheca* Rafin., *Vallea* Multis ex L. f., and *Xyris* L. The majority of these taxa are predominant in the present-day Andean forest and páramo vegetation (van der Hammen & Cleef, 1986; Cleef et al., 1993).

During the late Pliocene (Biozone III), continued uplift increased elevation to ca. 2600 m. About 40% of the fossil flora taxa have a tropical affinity and 35% have a temperate affinity. The Amazonian-centered families and the Andean-centered and Laurasian elements contribute 18% and 60%, respectively, to the paleoflora. The main forest taxa, including *Alchornea* Sw., *Hedyosmum* Sw., *Myrica* L., Podocarpaceae; *Weinmannia* L., *Hesperomeles* Lindl., *Myrica* L., *Rubus* L., and *Turpinia* Vent., are recorded for the first time. The composition of the late Pliocene Andean forest differs from that of the late Quaternary Andean forest. Notable is the absence of *Alnus* Mill., *Juglans* L., and *Quercus* L., which immigrated into the area during the Pleistocene. The contribution of *Hedyosmum*, *Myrica*, and Podocarpaceae to the Andean vegetation cover was apparently higher in the late Pliocene than in the Quaternary (Wijninga & Kuhry, 1993). It is possible that the late Pliocene forest had a more open character locally (in the area of the high plain of Bogotá), perhaps related to a dynamic river valley environment (Hooghiemstra, 1984; Torres et al., 2005). To some extent, the above-mentioned characteristics of this early Andean forest are already apparent during the middle Pliocene (Biozone IIB) and prevail until the early Pleistocene.

During the Quaternary, repeated climate change forced main vegetation belts to migrate altitudinally along mountain slopes. Combining the palynological information from ecotone forests (e.g., van der Hammen, 1974; van't Veer & Hooghiemstra, 2000) with the dynamics at lower elevations (Wille et al., 2001), we concluded that the subandean forest belt was maximally squeezed, during glacial periods in particular, from the present-day ca. 1300 m vertical extension (ca. 1000–2300 m) to ca. 600 m vertical extension during the Last Glacial Maximum (LGM) (ca. 800–1400 m). Other vegetation belts lost less of their vertical expansion during the LGM: tropical lowland forest lost 200 m (0–800 m LGM expansion) and Andean forest lost 300 m (1400–2000 m LGM expansion). The páramo belt kept the same altitudinal extension (2000–3000 m) during the LGM as today, but this belt in particular gained much surface when it moved to lower elevations. In consequence, Quaternary dynamics were highest in the páramo belt. This reconstruction is consistent with the observation that the high mountain flora, in particular, reached a high level of diversity. In the Espeletiinae group, highest diversity occurs in the area where the uplift history is youngest (Cuatrecasas, 1979), suggesting that in the northern Andes the dynamic Quaternary environment has contributed positively to the present-day high level of plant diversity.

Conclusions

- Differences in the composition of fossil plant associations recovered from sediments in the area of the Bogotá basin form a series from middle Miocene to late Pliocene and reflect changing climatic conditions that result primarily from the Pliocene tectonic uplift of the Eastern Cordillera.
- Global temperature change during the Neogene, estimated at 3°C, may explain at most one third of the difference in inferred paleoaltitude, and hence the difference in floristics between the oldest and youngest fossil plant assemblages.
- The fossil plant assemblages show that the late Miocene vegetation was dominated by taxa with a wide tropical or neotropical distribution. Early montane forest seems to have been relatively rich in Podocarpaceae. During the Pliocene, the diversification of the forests gradually increased. Taxa with a cosmopolitan, wide temperate, tropical amphipacific, or Holarctic distribution enhanced the diversity of the montane forest. During the same time span, the number of Amazonian-centered families decreased in favor of families of Laurasian origin.
- Although reconstructed forest types are non-analogues, to a certain extent they can be compared to their modern homologues, taking into consideration the absence of taxa that immigrated into the study area at a later time.
- Although in some parts of the Eastern Cordillera uplift had already started in the middle Miocene, the area of Bogotá remained below 700 m altitude until the late Miocene.
- From the middle Pliocene onward, the number of Holarctic and Asia-derived (e.g., *Trigonobalanus* Forman, *Symplocos* Jacq.) taxa increased. This indicates the importance of the northern migration route via the Panamanian isthmus for plant taxa. Migration from southern South America possibly occurred before the late Neogene. A substantial number of Austral-Antarctic taxa arrived in the northern Andean montane rain forest biome before immigration from the Northern Hemisphere took place, but in the present-day flora there are fewer immigrants from the south than from the north.

- Based on the studied fossil plant assemblages, the first records of páramo-like vegetation are from the late Pliocene, confirming earlier conclusions by van der Hammen et al. (1973).
- Mainly during the Quaternary, climate change forced vegetation belts to migrate vertically. During this process, vegetation belts were repeatedly squeezed in altitudinal extension and afterward expanded again, causing populations to be repeatedly isolated and remerged. In the northern Andes, high diversity correlates strongly with a dynamic environment in which migration and isolation played key roles.

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Appendix 1. Checklist of identified pollen taxa, their phytogeographic relationships, and their absence/presence in the studied pollen and macrofossil floras. Sites: S. de T. I/II = Salto de Tequendama I/II (middle Late Miocene); Río F 17 = Río Frio-17 (early Pliocene); Subach. 39 = Subachoque-39 (early Pliocene); Faca. 13 = Facatativá-13 (middle Pliocene); Guasca 103 (late Pliocene). Modern phytogeographic units: 1 = wide tropical; 2 = tropical Africa-America; 3 = neotropical; 4 = tropical amphipacific; 5 = wide temperate; 6 = austral-antarctic; 7 = holarctic; 8 = andean neotropical; 9 = cosmopolitan. (cf. genus name = sp. ined., cf. genus name). Appendix modified after Wijninga (1996d).

Taxon	Phyt. unit	S.de T. I/II	Rio F 17	Subach. 39	Faca. 13	Guasca 103
Acacia Miller	1	x				
Acalypha L.	1				x	x
Acanthaceae	1	x			x	
Alchornea Sw.	1	x	x	x	x	x
Alismataceae	9	x			x	x
Amanoa Aubl.	3	x	x	x		
Anacardiaceae	1			x		
Anacardium L. cf.	3	x				
Annonaceae	1	x				
Anthurium Schott.	3	x				
Antidaphne Poeppig & Endl.	3				x	x
Apiaceae	9	x			x	x
Apocynaceae	1	x		x	x	
Araliaceae	1			x	x	
Arecaceae (Palmae)	1	x	x		x	x
Artemisia L.	7				x	
Asplundia Harling cf.	3	x				
Asteraceae - liguliflorae	9	x			x	
Asteraceae - tubuliflorae	9	x	x	x	x	x
Astrocaryum G. Meyer	3	x	x			
Azolla Lam.	9		x			x
Bactris Jacq. Ex Scop.	3	x				
Bauhinia L.	1			x		
Bernouillia Oliver	3	x				
Bignoniaceae	1				x	
Billia Peyr.	3			x		x
Bocconia L.	4				x	
Bomarea Mirbel	8				x	
Bombacaceae	1	x	x	x		x
Bombacopsis Pittier	3				x	
Borreria G. Meyer	6					x
Bromeliaceae	3				x	
Brownea Jacq.	3	x				
Bursera Jacq. ex L.	3			x		
Byrsonima Rich. ex Kunth	3			x		
Byttneria Loefl.	1	x				
Calceolaria L.	1				x	
Callitriche L.	5				x	x
Carex L.	5				x	x
Catopsis Griseb.	3	x				
Catostemma Benth.	3	x				
Cecropia Loefl.	3	x	x	x	x	x
Cedrela P. Browne	3	x		x	x	
Ceiba Miller	1	x				
Celtis L.	7				x	
Chrysobalanaceae cf.	1	x				
Clethra L.	4	x		x	x	x
Clusia L.	3	x		x	x	x
Clusiaceae s.l. (Guttiferae)	9	x		x		
Convolvulaceae	9	x				
Connarus L. cf.	1	x				
Cordia L.	1	x				
Coussapoa Aubl.	1					x
Crassoretitriletes	1	x				
Croton L.	1	x		x	x	

Appendix 1. Continued.

Taxon	Phyt. unit	S.de T. I/II	Rio F 17	Subach. 39	Faca. 13	Guasca 103
Cyatheaceae	1	x	x	x	x	x
Cydista Miers	3					x
Cyperaceae	9	x	x	x	x	x
Cystopteris Bernh.	7				x	
Dalechampia L.	1	x				
Daphnopsis C. Martius	3				x	
Decussocarpus Laubenf.	1					x
Dicksonia L'Hér.	4				x	
Duroia L.f.	3	x				
Ecclinusa C. Martius	3	x				
Eleocharis R. Br.	9					x
Ericaceae	9	x			x	
Eugenia L.	1	x		x	x	
Euphorbiaceae cf.	9	x		x	x	
Evodianthus Oersted. cf.	3	x	x		x	
Fabaceae	9	x		x	x	
Faramea Aubl.	3	x			x	
Ficus L.	1	x			x	
Freziera Willd.	8		x	x	x	
Fuchsia L.	6					x
Gaiadendron G. Don f.	8				x	
Guarea Allam ex L.	2			x	x	
Gunnera L.	6			x		x
Hedyosmum Sw.	4	x	x	x	x	x
Hesperomeles Lindley	8					x
Hippocratea L./*Pristimera* Miers	1					x
Humiriastrum (Urban) Cuatrec.	3	x		x		
Hyeronima Allemão	3	x		x	x	x
Hypericum L.	5			x	x	x
Ilex L.	9	x	x	x	x	x
Ipomoea L.	1					x
Iriartea Ruiz & Pavón	3	x	x	x	x	
Iridaceae	9	x				
Juncaceae s.l.	9	x				
Juncus L.	5	x	x		x	x
Lathyrus L.	7				x	
Lepidium L.	9					x
Loranthaceae	9	x			x	x
Ludwigia L.	9	x	x		x	x
Lycopodium L.	9	x		x	x	x
Lythraceae	9				x	x
Mabea Aubl.	3				x	
Machaerium Pers. cf.	3	x				
Macoubea Aubl. cf.	3	x	x	x		
Macrocarpea (Griseb.) Gilg	8				x	
Macrolobium Schreber	3	x	x	x	x	
Malpighiaceae	1	x		x	x	x
Malvaceae	9				x	
Mauritia Kunth	3	x	x	x		
Melastomataceae	1	x	x	x	x	x
Meliaceae	1	x		x	x	
Monnina Ruiz & Pavón	3				x	
Montia L.	5				x	x
Muehlenbeckia Meissner	6			x		
Myrica L.	7				x	x
Myriophyllum L.	9				x	
Myrsine L.	1			x	x	x
Myrtaceae	1	x	x	x	x	x
Oreopanax Decne. & Planchon	3				x	x
Paraprotium-type Cuatrec.	3			x		

Appendix 1. Continued.

Taxon	Phyt. unit	S.de T. I/II	Rio F 17	Subach. 39	Faca. 13	Guasca 103
Parinari Aubl.	1	x		x		
Passiflora L.	3	x				
Piperaceae	1				x	
Pityrogramma Link	2	x				
Poaceae	9	x	x	x	x	x
Podocarpaceae	6	x			x	x
Podocarpus L'Hér. ex Pers.	6	x	x	x	x	x
Polygonum L.	5	x			x	x
Pouteria Aubl.	1	x			x	
Protium Burm.f.	1	x			x	
Pseudobombax Dugand	3	x				
Psychotria L. cf.	1	x				
Quararibea Aubl.	3				x	
Ranunculus L.	5					x
Rheedia L.	2	x				
Rhus L.	7			x	x	
Rubiaceae	9	x		x	x	x
Rubus L.	5					x
Rumex L.	5				x	
Sacoglottis C. Martius	3	x	x	x		
Sagittaria L.	9	x				
Salix L.	7			x		x
Salvia L.	7	x			x	
Salvinia Séguier	1	x				
Sapindaceae	1	x		x		
Sapium P. Browne.	3			x	x	
Sapotaceae	1	x				
Schefflera Forster & Forster f.	3	x		x	x	x
Scirpus L. cf.	9	x				
Selaginella Pal.	9	x		x	x	
Sericotheca Rafin.	3				x	
Solanaceae	9			x	x	x
Spathiphyllum Schott	3	x	x			
Sphagnum L.	9					x
Symplocos Jacq.	4	x	x	x	x	x
Tapirira Aubl.	3	x				
Thelypteris Schmidel	5			x		
Thoracocarpus Harling cf.	3	x				
Tiliaceae	9	x				
Tournefortia L.	1				x	
Trichantera Kunth / *Bravaisia* D.C.	3				x	
Tristerix Mart.	3			x	x	
Turpinia Vent.	4					x
Typha L.	9			x		x
Urticaceae	9				x	x
Urticales	9	x	x	x	x	x
Valeriana L.	5			x	x	
Vallea Mutis ex L. f.	8				x	
Vantanea Aubl.	3	x		x		
Viburnum L.	7			x		x
Virola Aubl.	3	x				
Vismia Vand.	3			x		
Vochysia Aubl.	3	x				
Warszewiczia Klotzsch	3	x		x	x	
Weinmannia L.	6			x	x	x
Xylosma Forster f.	1			x		
Xyris L.	1				x	x
Zanthoxylum L.	1			x		x

PALEOBOTANICAL EVIDENCE AND MOLECULAR DATA IN RECONSTRUCTING THE HISTORICAL PHYTOGEOGRAPHY OF RHIZOPHORACEAE[1]

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Abstract

The fossil record of the Rhizophoraceae includes numerous questionable identifications from strata of unconfirmed age, together with others representing clear evidence of the family in deposits whose age is well constrained by independent or multiple lines of evidence. *Bruguiera* or the *Bruguiera* lineage, and *Ceriops* are known from the early Eocene, *Kandelia* from the middle Eocene, and *Rhizophora* from the late Eocene. *Combretocarpus* is likely present by the middle Miocene, but it belongs to a family (Anisophylleaceae) earlier placed in the Rhizophoraceae that is now considered unrelated to that family. *Rhizophora*, as a genus, has existed essentially uninterruptedly in the Caribbean region since the late Eocene, but cooling events at ca. 15–14 Ma, ca. 3.4 Ma, and ca. 1.6 Ma, and the subsequent 18 to 20 glacial intervals provide a mechanism for development of the cold(er) tolerant populations toward the northern part of its range in the New World. In reconstructing the biogeographic history of *Rhizophora* in the Caribbean region, it is worthwhile noting that molecular-defined lineages (with little morphological or palynological variation) may have been introduced and gone extinct on multiple occasions. This allows for variation in molecular patterns and apparent stasis in the fossil record—a possibility not widely considered in the literature. The most recent molecular-defined common ancestor to existing populations is estimated to have arrived in the New World ca. 11 Ma, using an origin in the Paleocene (ca. 60 Ma) as the basis for calculation.

Key words: fossils, historical phytogeography, Rhizophoraceae.

Resumen

El registro fósil de Rhizophoraceae incluye numerosas identificaciones cuestionables de estratos sin edad confirmada, junto con otros que representan clara evidencia de que la familia se encuentra en depósitos cuya edad está forzada por líneas de evidencias independientes o múltiples. *Bruguiera* o el linaje *Bruguiera*, y *Ceriops* se conocen del Eoceno temprano, *Kandelia* del Eoceno medio y *Rhizophora* del Eoceno tardío. *Combretocarpus* está presente probablemente a partir del Mioceno medio, pero pertenece a una familia (Anisophylleaceae) ubicada anteriormente en Rhizophoraceae que ahora se considera sin relación a esa familia. *Rhizophora*, como género, ha existido esencialmente sin interrupción en la región del Caribe desde el Eoceno tardío, pero eventos de enfriamiento hace ca. 15–14 Ma, ca. 3.4 Ma y ca. 1.6 Ma, y los subsecuentes 18 a 20 intervalos glaciales proporcionan un mecanismo para el desarrollo de poblaciones tolerantes al frío hacia la parte norte de su distribución en el Nuevo Mundo. Al reconstruir la historia biogeográfica de *Rhizophora* en la región del Caribe, cabe observar que linajes moleculares (con poca variación morfológica o palinológica) pudieron haber aparecido y extinguido en múltiples ocasiones. Esto permite la variación en patrones moleculares y aparente estasis en el registro fósil – una posibilidad no ampliamente considerada en la literatura. El antepasado común de definición molecular más reciente de las poblaciones existentes se estima que llegó al Nuevo Mundo hace ca. 11 Ma, si se usa un origen en el Paleoceno (ca. 60 Ma) como la base para el cálculo.

Investigations of fossil *Rhizophora* L. in the Caribbean, in association with studies on phylogeny (Schwarzbach & Ricklefs, 2000), have led to this review of reports of the family Rhizophoraceae worldwide. One purpose of the review is to discern from the numerous reports of Rhizophoraceae, from strata purportedly ranging in age from the Cretaceous to the Recent, identifications and ages that afford a reliable basis for reconstructing the evolution and historical biogeography of the family. From that base, the gradual accumulation of new evidence from genes, molecules, morphology, and fossils will allow continuing revision in concepts, and the increasing integration of the historical record with biogeographic and phylogenetic patterns derived from modern systematic approaches.

Modern Distribution and Global Fossil Records of Rhizophoraceae

The circumscription of extant Rhizophoraceae and Anisophylleaceae (included within the Rhizophoraceae by some authors; e.g., Melchior, 1964) is listed in

[1] Information on molecular systematics was provided by Andrea Schwarzbach from on-going studies by her and collaborators on the Rhizophoraceae, and on the fossil records by Aaron M. Ellison, Jeri Kvacek, M. K. Macphail, and Peter Saenger. The manuscript was read by Robyn J. Burnham, Aaron M. Ellison, Shirley A. Graham, and Andrea Schwarzbach.

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Table 1. Circumscription of Rhizophoraceae and Anisophyllaceae by various authors as given in Schwarzbach and Ricklefs (2000). * indicates genera reported in the fossil record.

Rhizophoraceae
Macarisieae
Anopyxis Pierre ex Engl.
Blepharistemma Wall. ex Benth.
Cassipourea Aubl.
Comiphyton Floret
Dactylopetalum Benth.
Macarisia Thou.
Sterigmapetalum Kuhlm.
Gynotrocheae
Carallia Roxb.
Crossostylis J. R. Forst. & G. Forst.
Gynotroches Blume
Pellacalyx Korth.
Rhizophoreae
**Bruguiera* Lam.
**Ceriops* Arn.
**Kandelia* (DC.) Wight & Arn.
**Rhizophora* L.
Anisophylleaceae
Anisophyllea R. Br.
**Combretocarpus* Hook. f.
Poga Pierre
Polygonanthus Ducke

Table 1. It is noted that the Anisophylleaceae is recognized as a separate and unrelated family by Schwarzbach & Ricklefs (2000), and of the 15 genera included in the Rhizophoraceae, only four (tribe *Rhizophoreae*) are exclusively mangroves.

Only five of these genera have been reported in the fossil record. For some, the age of the strata has not been firmly established, the identifications have not been confirmed or have been questioned, and broad or tentative identifications by the original author(s) have achieved greater certainty with repetition in the later literature. For purposes of biogeography, paleoenvironmental reconstructions, tracing lineages, and calibrating molecular data for taxa in which there is a relatively extensive fossil record, it is useful to have one set of paleobotanical evidence limited to reports in which the taxonomic level of the identifications is unambiguous, the age of the strata is well established, and the implications of the record are conservatively interpreted. For the Rhizophoraceae this record begins in the early Eocene (ca. 50 Ma; million years, millions of years ago), and for *Rhizophora* it begins in the middle to late Eocene (ca. 45 Ma; Table 2). The incorporation of more tentative data allows development of further theories and models of interest provided the assumptions, speculations, and acceptance of provisional identifications are clearly designated. This more inclusive record for the Rhizophoraceae and *Rhizophora* extends the range into the Paleocene (ca. 60 Ma; e.g., Gruas-Cavagnetto, 1976; Thanikaimoni, 1987). Where both kinds of evidence are part of the overall record, it is worthwhile to have two calculations that bracket the potential evolutionary history of the lineage.

Pollen of the *Combretocarpus*-type (Anisophyllaceae; Muller, 1981) was recovered from late Miocene deposits in northwestern Borneo (Anderson & Muller, 1975). A single grain was found in the Miocene Berakas coal, and the pollen became frequent in the Holocene Marudi peat. Morley (1977) found it in the middle Miocene of the same area. Thus, if the family has a fossil record, and this has not been established, it consists of pollen of the *Combretocarpus*-type, possibly representing the Anisophylleaceae, from the middle Miocene to Holocene of Borneo. If the pollen is *Combretocarpus*, and knowing that the original author (Muller, 1964) did not report it from other material studied from Borneo, the Maracaibo region of northern South America, or from extensive projects by Bataafse Internationale Petroleum Maatschappij (Shell Oil Company) in Nigeria and elsewhere (Germeraad et al., 1968), it is reasonable to assume that the middle Miocene marks the early appearance of *Combretocarpus* of the Anisophylleaceae. This is younger than the minimum age for the Rhizophoraceae (see below), and it will be interesting to see if this temporal sequence of the two families, and its phylogenetic implication, remain true with further phylogenetic and paleobotanical study.

In the Rhizophoraceae, fruits of *Kandelia* Wight & Arn. are reported from the middle Eocene of Alaska (Wolfe, 1972, 1977). A hypocotyl of † (= fossil) *Ceriops cantiensis* is reported from the London Clay flora of England (early Eocene, Ypresian; 52–49 Ma (Collinson, 1983)), and pollen is reported from the late Miocene of the Marshall Islands (Leopold 1969; listed as pending in Muller, 1981) and possibly from the late Eocene of southwestern Australia (Churchill, 1973). The latter is not a definite report of *Ceriops*, but the author regarded it as possibly present among the abundant and morphologically similar *Rhizophora* pollen. Hypocotyls resembling *Bruguiera* are known from the London Clay and are identified as †*Palaeobruguiera* (Collinson, 1983). Starch grain casts and molds similar to those of modern *Ceriops* and *Bruguiera* have also been found in the London Clay (Wilkinson, 1983). Reports of fossils with uncertain generic identifications include pollen similar to *Rhizophora* or *Kandelia* from the earliest Eocene of France (Gruas-Cavagnetto et al., 1988) and *Bruguiera*-type pollen of the same age in the Paris Basin

Table 2. Reports of *Rhizophora* in the fossil record of the Caribbean region. Fm(s)=formation(s). BP = before present.

Age/formation	Locality	References
Eocene/El Bosque, La Trinidad Fms	Chiapas, Mexico	Tomasini-Ortiz & Martínez-Hernández, 1984
Middle to Late Eocene/Gatuncillo Fm	Panama	Graham, 1985
Late Eocene to Present	Maracaibo Basin, Venezuela	Germeraad et al., 1968; Lorente, 1986
Oligocene	Colombia	Lorente, 1986
Middle Oligocene/San Sebastian Fm	Puerto Rico	Graham & Jarzen, 1969
Middle Oligocene/San Sebastian Fm	Puerto Rico	Hollick, 1928
Oligocene to Present	Brazil	Lorente, 1986
Oligocene to Miocene	Colombia	Lorente, 1986
Early Miocene/Culebra, Cucaracha, La Boca Fms	Panama	Graham, 1988a, b, 1989
Early Miocene/La Quinta Fm	Chiapas, Mexico	Langenheim et al., 1967; Graham, 1999c
Early Miocene/Ixtapa Fm	Chiapas, Mexico	Martínez-Hernández, 1992
Early to Middle Miocene	Venezuela	Lorente, 1986
Early to Middle Miocene	Venezuela	Berry, 1922
Early to Late Miocene	Brazil/Colombia	Hoorn, 1994a, b, c
Late Miocene/Gatun Fm	Panama	Graham, 1991a, b
Pliocene/Herrería Fm	Guatemala	Graham, 1998
Middle Pliocene/Paraje Solo Fm	Veracruz, Mexico	Graham, 1976
Middle Pliocene/Uscari Fm (age fide Collins to Burnham, pers. comm.)	Costa Rica	Graham, 1987
Quaternary		
Late glacial-Holocene	Yucatan Peninsula	Leyden et al., 1994
Holocene	Middle American Trench, Tehuantepec, Mexico	Habib et al., 1970
Holocene	Isla Juventud, Cuba	Moncada Ferrera et al., 1990–1991
35,000 yrs BP	Gatun Lake, Panama	Bartlett & Barghoorn, 1973
12,000 yrs BP	Gatun Lake, Panama	Bartlett & Barghoorn, 1973
7000 yrs BP	Playa Medina, NE Venezuela	Vegas & Rull (in ms.)
5100 yrs BP	Bragança Peninsula Pará, Brazil	Behling et al., 2001
Holocene	Trinidad	Berry, 1925
Holocene	Brazil [Other reports of Rhizophoraceae/*Rhizophora* from Latin America][1]	Behling, 1996
Paleocene/Cerro Boraró Fm	Chubut, Argentina	Petriella, 1972[2]
Late Eocene to Early Oligocene/Potoco Fm	Altiplano, Bolivia	Horton et al., 2001[3]

[1] Various reports of pollen from the Paleocene to Eocene of northern South America by van der Hammen & Wijmstra (1964) and Wijmstra (1971) are now assigned by the authors to the late Eocene or younger. Another South American record is †*Zonocostites ramonae* (pollen) from various sites on the continental platform off eastern Brazil, Late Cretaceous to Oligo-Miocene, in a technical report by Pares Regali et al. (1974a).

[2] Tentative reference of generalized wood to Rhizophoraceae.

[3] †*Zonocostites ramonae*, biological affinities are not cited by the author.

and in southern France (Gruas-Cavagnetto, 1991; Gruas-Cavagnetto et al., 1980). Pollen of *Bruguiera*-type (see *B. gymnorhiza*) is reported from the late Miocene of the Marshall Islands (Leopold, 1969; considered pending by Muller, 1981), and from the Oligocene of England (*Bruguiera parviflora* (Roxb.) Wight & Arn.-type; Machin-Pallot, 1971). With regards to the latter, Muller (1981: 63) notes that "Careful comparison failed to confirm this identification. Points of difference are the more prolate shape, less pronounced costae along the colpi, the indistinct endoaperture and thin, psilate exine." Among members of the Rhizophoraceae, those with the most convincing fossil record are *Kandelia* from the late middle Eocene of Alaska (Wolfe, 1972, 1977), and *Ceriops* and *Bruguiera* both from the early Eocene of England (Collinson, 1983; Wilkinson, 1983) and the Miocene of the Marshall Islands (Leopold, 1969).

The earliest fossil record of *Rhizophora* is difficult to establish because of the uncertainty of some identifications and the unsettled age of some strata. Several geologic range charts have been published that include *Rhizophora* (Germeraad et al., 1968; Rico-Gray, 1993; Saenger, 1998; Ellison et al., 1999;

Morley, 2000), and summaries are available of the global record (Muller, 1981; Plazait et al., 2001) and of more specific areas: Mexico (Langenheim et al., 1967), the Caribbean Basin region (Graham, 1995), Maracaibo Basin (Rull, 1998), the southeastern Pacific (Hekel, 1972; Churchill, 1973; Anderson & Muller, 1975; Mepham, 1983; Ellison, 1991), and India (Prakash, 1960; Thanikaimoni, 1987).

Muller (1981: 62) was of the opinion that, "The oldest records [of *Rhizophora*] are still the upper Eocene occurrences of *Zonocostites ramonae* Germeraad, Hopping & Muller reported by Germeraad, Hopping, and Muller (1968) from the Caribbean area and confirmed by Pares Regali, Uesugui, and Santos (1974a, b) in Brazil." Several older records were rejected by Muller: the middle Eocene of India (Venkatachala & Rawat, 1972, 1973), because the basis for the age assignment is unclear, "and since the subzone is the uppermost one, an upper Eocene age appears possible" (Muller, 1981: 63); the Paleocene and lower Eocene of western Europe (Gruas-Cavagnetto, 1976; Krutzsch, 1969, 1970; Krutzsch & Vanhoorne, 1977), because the authors allied †*Tricolporopollenites mansfeldensis* with *Rhizophora* on the basis of similarities in morphology that were questioned; and the Cretaceous (Maestrichtian) of Canada (*Rhizophora*-type; Jarzen, 1978), because the fossils are characterized by much wider endoapertures, lack of polar costae, lack of colpi, and have a uniform granular structure. A record in the Ilerdien or Ypresian (earliest Eocene) of "Rhizophoraceae?" from the Pyrenees region (Gruas-Cavagnetto et al., 1988: 221) is uncertain because distinct colpi transversalis are not evident in the photograph; it should be noted that the specimens are identified in the text as "Rhizophoraceae?" while on the range chart the question mark does not appear (Gruas-Cavagnetto et al., 1988: 221 and 222, respectively). In the IOP (International Organization of Palaeobotany) Plant Fossil Record Data Base (www.biodiversity.org.uk), the Ilerdien/Ypresian record is listed under Rhizophoraceae as ?first occurrence.

There are reports of Rhizophoraceae in even older deposits in the early literature, but none of these have been confirmed: †*Rhizophorites bombacaceus* Bayer (leaf, affinites cited as with Rhizophoraceae) from the Cenomanian (early late Cretaceous) of Bohemia (Bayer, 1914) and †*Rhizophorocarpus dekapetalus* Velenovský & Viniklář (fruit, Rhizophoraceae) from the Cretaceous of Bohemia (Velenovský & Viniklář, 1926) as listed in the Andrews (1970) catalog. No pre-late Eocene records for the family or the genus *Rhizophora* are listed in the LaMotte (1952) catalog. The Bohemia fossils would be older by 50 Ma or more than any confirmed Rhizophoraceae. The specimen of *R. dekapetalus* is in the National Museum in Prague (J. Kvacek, pers. comm.); the location of *R. bombacaceus* is unknown. Neither genus is regarded as belonging to the Rhizophoraceae by Kvacek, who is working on the Bohemian Cretaceous floras, and he notes (pers. comm.) that in almost every case the generic determinations by Bayer and particularly Velenovský are proving incorrect.

The same concerns raised by Muller (1981) about the original identifications, subsequent confirmation or acceptance of the identifications, and/or age of the strata also apply to other pre-late Eocene reports listed in the range charts previously mentioned. These include *Rhizophora* from the Paleocene (Thanikaimoni, 1987) and early Eocene (Prakash, 1960; Lakhanpal, 1970) of India. The author's efforts to communicate about the status of the India specimens were not successful.

Rhizophora was reported from Borneo in beds initially assigned to the middle Eocene (Muller, 1964), but the age was later emended to the late Eocene by Muller (1981). In the Australasian region in general, and in Australia in particular where the Cenozoic plant microfossil record is extensive, "the earliest Rhizophoraceae (*Zonocolpites ramonae*) are middle late Eocene from the offshore Browse Basin in NW Australia" (MacPhail, pers. comm.; MacPhail, 1999). This is in contrast to older records (late Paleocene (60 Ma), and early Eocene (50 Ma)) from Australia and India cited in the summary by Saenger (pers. comm.; Saenger, 1998).

Considering the critical importance of the earliest records of a lineage in deciphering its phylogeny and biogeography, a conservative reading of the evidence is warranted. *Rhizophora*, as a modern genus reflected by the morphology of its pollen and its mangrove habitat, is first known in the late Eocene and appears almost simultaneously in the Old and New World tropics. This implies an earlier origin for the genus, possibly in the southeast Asia–eastern Tethys Sea region (Raven & Axelrod, 1974; Ellison, 1991), and the change from its absence in the middle Eocene to its dominance in many tropical coastal habitats in the late Eocene suggests rapid migration, and an origin in, or a rapid adjustment to, its present specialized habitat.

Among genera of Rhizophoraceae, *Rhizophora* appears somewhat later (late Eocene) than *Kandelia* (late middle Eocene) and *Ceriops/Bruguiera* (early Eocene), according to the data presented. However, the sequences of appearance are geologically close in time, and additional paleobotanical information and phylogenetic studies are needed to establish the time, place of origin, diversification, and radiation of the family.

THE CARIBBEAN FOSSIL RECORD OF *RHIZOPHORA* (TABLE 2)

Confidence that advancement has been made in understanding complex biological systems is enhanced when results from two independent lines of inquiry are congruent. Opportunity for achieving a new paradigm is presented when incongruous or partially incongruous data sets are reconciled, or when one data set limits the choices or supports a single interpretation from among several generated by another approach. Investigations into the historical biogeography of *Rhizophora* in the Caribbean region through paleobotanical techniques and by molecular approaches provide such an opportunity for discovering consistencies in interpretation, identifying apparent inconsistencies, and formulating hypotheses to explain the differences. There is clearly much left to do, as is evident, for example, from the view expressed by Ellison et al. (1999: 95) that "...regional species diversity [of mangroves] resulted from *in situ* diversification after continental drift" and by Plaziat et al. (2001: 1961) that "It is therefore clear that continental drift had a limited role in the dispersal and development of modern mangrove floras." The Caribbean region is a suitable place for comparing the fossil record with speciation models derived from molecular systematics, because the history of *Rhizophora* there is one of the best documented in the world.

A scenario for the origin and spread of the mangrove lineage (4 of 15 genera) within the Rhizophoraceae, based on interpretation of presently available molecular data, and augmented by information from the fossil record, is presented by Schwarzbach & Ricklefs (2000, 2001). The essentials of that scenario, as it relates to the Caribbean Basin, are as follows:

(1) *Rhizophora* reached the New World about 40 Ma (based on evidence from the fossil record).
(2) The genus underwent range contraction and extinction in the late Tertiary associated with cooling climates (evidence for cooling climates is based on the fossil record and other geological evidence).
(3) The genus may have disappeared from the Atlantic and Caribbean regions (a possible interpretation of the molecular data).
(4) If so, *Rhizophora* was probably re-introduced about 11 Ma (a possible interpretation of the molecular data using a date of 60 Ma for the origin of the family).

To better constrain the time during which *Rhizophora* most likely would have disappeared from the Caribbean region ("the late Tertiary, probably associated with cooling climates" (Graham, 1999a: 87)), the following summary is presented of the relevant global paleoclimatic trends as a context for assessing the Caribbean record. Beginning with the end of the hot house interval near the early Eocene/middle Eocene boundary (ca. 52 Ma):

Early Eocene—earliest mountain glaciers first appeared on Antarctica (Birkenmajer, 1990),
Late middle Eocene and early Oligocene—limited ice sheets appeared along the margin of Antarctica (Leg 119 Shipboard Scientific Party, 1988),
Early/late Oligocene boundary (ca. 30 Ma)—more extensive ice developed on Antarctica (Miller et al., 1987; Poore & Matthews, 1984), as reflected in a major drop in global mean sea level (see Graham, 1999a: 95),
Middle Miocene (15–14 Ma)—permanent ice formed on Antarctica and glacial climates developed in the Arctic,
Middle Pliocene (ca. 3.4 Ma)—extensive northern hemisphere glaciation began (Shackleton & Opdyke, 1977),
Quaternary (ca. 1.6 Ma)—ice age began; present interglacial began ca. 11 Kyr (thousand years, thousands of years ago).

If cooling climate was a factor in the possible disappearance of *Rhizophora* from the Caribbean region in the late Tertiary, 15–14 Ma would be a likely time as shown by the initiation of permanent ice on Antarctica, glacial climates in the Arctic region, and a number of terrestrial vegetational responses on a global scale (e.g., the trend toward replacement of forest by grasslands in mid-continent North America (Graham, 1999a) and the disappearance of warm elements from the flora of New Zealand (Lee, pers. comm.)). Beginning about this time, changes also occurred in the vegetation of northern Latin America that would be consistent with, and reciprocal to, a restriction in the range of *Rhizophora* due to cooling climates. The principal change was the introduction of an increasing number of northern temperate elements progressively farther south into the lower latitudes (*Abies* Mill., *Picea* A. Dietr., *Pinus* L., *Alnus* L., *Celtis* L., *Fagus* L., *Juglans* L., *Liquidambar* L., *Myrica* L., *Populus* L., *Ulmus* L.; Graham, 1999b). These events identify the most likely beginning for any disappearance of *Rhizophora* from the Caribbean region at 14–15 Ma. The 3–4 Ma period between 14–15 Ma and *Rhizophora*'s estimated return at ca. 11 Ma corresponds to the Serravallian Stage of the middle Miocene (10.4–14.2 Ma; Harland et al., 1989), and is part of the 'ice house' interval when global climates were becoming cooler. In the combined analyses by Schwarzbach & Ricklefs (2000, 2001; Schwarzbach, pers. comm.), a maximum age of 60 Ma is used for the earliest *Rhizophora* from which a New World/Old World split in *Rhizophora*, and its reintroduction into the New World at 11 Ma is calculated. When the younger age of ca. 45 Ma is used (Schwarzbach, in prep., pers. comm.), bracketing the possibilities afforded by the fossil record, that split and any reintroduction into the New World has a younger dating. Thus, the initial appearance of

Rhizophora in the Caribbean and its subsequent record is of interest.

Beginning in the Quaternary, it is probable that the range of *Rhizophora* in the Caribbean region fluctuated with changes in temperature, salinity, and sea level (see Blasco et al., 1996). However, if *Rhizophora* disappeared as a consequence of the colder-than-at-present intervals of the past 2 Ma, then accommodation must be made for the likelihood of 18 to 20 of these presence/absence cycles, because that is the number of such cold intervals documented for the Quaternary Period in the northern latitudes (Milankovitch eccentricity cycles of 100 Kyr; see papers cited in Graham, 1999a: 37–41); the effect of these cold intervals on biotas is now known to have extended into the low latitudes, as shown by strontium/calcium ratio data from Barbados corals (Guilderson et al., 1994) and North Atlantic Heinrich events reflected in pollen sequences from south-central Florida (Grimm et al., 1993; see papers cited in Graham, 1999a: 283). There are no plant fossil-bearing sections that extend back into one or more of the glacial maxima in the Caribbean region to provide direct evidence of its history during the cold periods (e.g., at 18 Kyr). However, the paleobotanical evidence that is available suggests that *Rhizophora* did not disappear and return 18 to 20 times during the past 2 Ma in that region (Table 2). For example, sediment cores from Gatun Lake, Panama show that at ca. 35 Kyr *Rhizophora* pollen comprised 74% of the total palynomorph assemblage, and it has been present in varying amounts for the past 12 Kyr (Bartlett & Barghoorn, 1973). At any rate, brief, relatively recent, rapid, and partial range restrictions are not the kind needed to explain that aspect of the molecular data open to the possible interpretation of a 3–4 Ma absence from the Caribbean region between 15–14 to 11 Ma. The cooling events at 15–14 Ma, 3.4 Ma, 1.6 Ma, and the fast-paced glacial-interglacial fluctuations of the Quaternary Period do, however, provide a mechanism for the presence of cold(er) tolerant populations of *Rhizophora* in southern Florida, Jamaica, St. Croix, and Texas mentioned by Schwarzbach & Ricklefs (2001).

For the Tertiary, the question is whether it is a viable option, in interpreting the molecular data, to assume that *Rhizophora* was absent from the Caribbean region for a significant span of time after its initial appearance in the late Eocene. The Caribbean fossil record of *Rhizophora* is based on fossil pollen, known in the stratigraphic literature as *Zonocostites ramonae*. Numerous well cores have been drilled and examined extensively for plant microfossils in the petroleum-rich Caribbean Basin; *Rhizophora* pollen is distinctive and easily recognizable at the generic level (Langenheim et al., 1967; Muller & Caratini, 1977) and is an indicator of depositional environments—an important aspect of petroleum geology. For these reasons, the stratigraphic range of *Rhizophora* pollen in the Caribbean Basin is well known and can be confidently fixed as beginning in the late Eocene. The oldest occurrences are in the late Eocene Gatuncillo Formation of Panama, and the early to middle part of the late Eocene of Venezuela (Maracaibo Basin: Germeraad et al., 1968; Lorente, 1986), corresponding to a time period around 45–40 Ma.

Regarding the subsequent history of *Rhizophora*, Lorente (1986) studied a section from the late Tertiary of Venezuela that includes the interval from the early to middle Miocene (Burdigalian to Langhian), and *Zonocostites ramonae* is present throughout. It has also been reported from the Oligocene to Miocene of Colombia, from the Oligocene to the Recent of Brazil, and from the late Eocene to the Recent generally throughout northern South America (Germeraad et al., 1968; Lorente, 1986); in early (Graham, 1988a, b, 1989) and late (Graham, 1991a, b) Miocene deposits in Panama; and in Pliocene sediments from Mexico (Graham, 1976). In both published and unpublished studies, *Rhizophora* is almost universally present from the late Eocene to the Recent in pollen/spore-bearing sediments from coastal habitats throughout the Caribbean Basin, and there is no evidence for a 3–4 Ma gap between 15–14 and 11 Ma, or at any time in the post late Eocene record.

A second point based on paleontological evidence concerns a cause for a possible disappearance of *Rhizophora*, and the timing of its subsequent return. If cooling temperatures were a reason for its disappearance at 15–14 Ma, it must be noted that the global paleotemperature curve shows that it was even colder at 11 Ma (Graham, 1999a: 89). This makes it difficult to explain its re-introduction under conditions more severe than those purported to explain its disappearance. There are no abrupt, short-lived, extensive catastrophic events known for the Tertiary interval involved, and fossil records from other groups do not show a response to such an event. Habitat reduction is unlikely during the time under consideration, because coastal environments were expanding with the fall in sea levels as glaciers began to develop more extensively.

It is clear that phylogenetic information alone does not discriminate among all possible patterns, and information from the fossil record can help to limit the different options. Also, the fossil record can help discriminate between a continuous presence and periodic absences as a result of catastrophic events. In the case of a continuous presence there should be a relatively uninterrupted fossil record, while cata-

strophic events should produce gaps in that record, likely accompained by similar evidence from adjacent regions, and this evidence is not present.

However, there are several limitations that must be acknowledged in reconstructing the historical biogeography of *Rhizophora* based on evidence from fossil pollen. Its history (Graham, 1995) is derived from records that for any one region may be intermittent for several reasons. One is that many samples are derived from roadside, streamside, and surface mine exposures that are widely separated both geographically and stratigraphically. Another is that even in cores resulting from drilling operations, there are zones missing or barren of terrestrial plant microfossils because there are changes in depositional environments (e.g., inundation, marine regression and erosion), the complete section was not studied, or selected results were considered proprietary and unpublished. A third reason is that tropical pollen and spore-bearing lignites, clays, and siltstones may be lain down under different depositional environments. Those deposited at the coastal interface between terrestrial and marine habitats frequently contain *Rhizophora* pollen (e.g., the middle Pliocene Paraje Solo Formation of Mexico; the early Miocene Culebra, Cucaracha, and La Boca formations of Panama; the late Miocene (fide Collins, pers. comm. to Burnham) Gatun Formation of Panama; Table 2). Similar sediments, but deposited in inland swamps, or upland bogs and marshes, removed from the influence of marine waters, do not contain *Rhizophora* pollen (e.g., the late Miocene Padre Miguel Group of Guatemala). For these reasons, range charts with continuous lines (e.g., Germeraad et al., 1968, fig. 15) imply the continual presence of a taxon over millions of years, but this can be misleading because sections for the Tertiary are not sufficiently continuous to detect absences of several thousands or tens of thousands of years. For *Rhizophora*, however, the combined records reduce the possibility of an absence even for this duration.

Another limitation to the paleopalynological approach for the present study is the taxonomic level to which *Rhizophora* pollen can be recognized. It is important to note that lineages here refer to molecular-defined lineages; in terms of morphology, including pollen morphology, the genus is not readily subdivided into clearly recognizable taxa. Langenheim et al. (1967) and others have studied the morphology of *Rhizophora* pollen, and based on the complete geographic and morphologic range of the genus they have concluded that no ecological or taxonomic categories can be consistently recognized on the basis of pollen characters. This leaves open the possibility that different lineages, defined by molecular and/or non-pollen morphological characters, may have migrated in and out of the region, leaving no evidence of the fluctuations in the plant microfossil record. This possibility has not been widely emphasized in the literature tracing the geologic record of lineages, but it will be increasingly important as histories based on paleobotanical evidence are integrated with those derived from molecular studies. In the case of *Rhizophora*, the stenopalynous condition of the pollen allows for the possibility of repeated introductions and extinctions of molecular- and otherwise-defined lineages. However, the coarse resolution of the fossil record, sea-level and paleotemperatures trending in the wrong direction, and undetected or selective catastrophies cannot be invoked to support a prolonged absence of *Rhizophora*, as a genus, from the Caribbean region after the late Eocene.

According to the fossil record, *Rhizophora* has been widespread in the New World since its initial appearance in about the late Eocene. No major gaps are apparent in its distribution since that time, and there is no evidence for region-wide catastrophic events. The model around which consensus is developing is one that involves frequent extinction and reintroduction of molecular-defined lineages, and pollen that documents the presence of *Rhizophora*, as a genus, in the Caribbean region since the late Eocene. According to recent calibration data (Schwarzbach & Ricklefs, unpublished data) the most recent common ancestor or colonizer that spread throughout the New World arrived about 11 Ma and diversified in response to environmental change. Consistent with the model are the documented climatic fluctuations and changes in the physical environment (Graham, 2003a, b, c) now known to have affected the Caribbean region and the associated changes in sea level and ocean salinity concentrations resulting from rapid glacial and interglacial transitions. Results from molecular-based studies may assume (1) intuitively a Paleocene origin (ca. 60 Ma) for the family because of its distribution and diversity in the Eocene, and (2) an Eocene origin (ca. 45 Ma) based on a conservative reading of the existing fossil record. These bracket the plausible options, and define critical time intervals where additional, verifiable records should be sought.

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MODERN PROCESSES AND HISTORICAL FACTORS IN THE ORIGIN OF THE AFRICAN ELEMENT IN LATIN AMERICA

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Abstract

The combination of factors that account for present-day distributions of organisms is unique to individual lineages and varies over time. An observation relevant to some lineages at some point in their history is that hurricane frequency and intensity appears to be increasing with global warming. If so, then directional winds from Africa to the Caribbean region (the trade winds), from South America to Africa (the westerlies), the ocean currents they induce, and the transport of the floating islands they carry, were likely more intense during the generally warmer-than-present Tertiary Period and especially at peaks of exceptional warmth. These peaks occurred in the Paleocene/Eocene (65–45 Ma), in the early to middle Miocene (broadly between ~23–12 Ma), in the middle Pliocene (3–4 Ma), and probably extended slightly later in the lower latitudes. The Paleocene/Eocene interval includes the time when the distance between Africa and South America was one-half to two-thirds that of the present, and when the Greater Antilles island arc was first becoming emergent as increasing target areas for propagules. The second and third intervals of warming include the times when molecular evidence suggests divergence between several African and New World lineages. Thus, wind and ocean transport of organisms and propagules throughout the Tertiary, and especially at peaks of warmth, was likely a more important means of dispersal than would seem plausible under present conditions.

Key words: Africa, Caribbean, dispersal, dust transport

Resumen

La combinación de factores que explican la distribución actual de los organismos es única a los linajes individuales y varía a través del tiempo. Una observación relevante para algunos linajes en un cierto punto en su historia es que la frecuencia y la intensidad de huracanes parecen aumentar con el calentamiento global. De ser así, entonces los vientos direccionales desde África hacia la región del Caribe (los vientos alisios), desde América del Sur hacia África (los vientos del oeste), las corrientes oceánicas que inducen y el transporte de las islas flotantes que llevan, fueron posiblemente más intensos durante el período Terciario, generalmente más caliente que el presente, y especialmente durante los picos excepcionales de calor. Estos picos ocurrieron en el Paleoceno/Eoceno (65–45 Ma), en el Mioceno temprano a medio (ampliamente entre ~23–12 Ma), en el Plioceno medio (3–4 Ma) y probablemente se extendieron levemente más adelante a las latitudes más bajas. El intervalo de Paleoceno/Eoceno incluye el tiempo en que la distancia entre África y América del Sur era la mitad a dos tercios de la actual, y cuando el arco de las Antillas Mayores recién empezaba a emerger como área blanco para los propágulos. El segundo y el tercer intervalos de calentamiento incluyen los períodos en que la evidencia molecular sugiere divergencia entre varios linajes africanos y del Nuevo Mundo. Así, el transporte de los organismos y propágulos por viento y océano durante el Terciario, y especialmente durante los picos de calor, fue probablemente un medio más importante de dispersión de que parecería plausible en condiciones actuales.

An increasing number of plants with African affinities is being recognized in the Gulf/Caribbean and adjacent region. For example, the American Lythraceae genera *Crenea* Aubl. and *Ginoria* Jacq. have African origins (S. Graham, 2002). The Dominican amber has long been regarded as a product of the legume *Hymenaea* L., but Hueber and Langenheim (1986) have shown that rather than being produced by the widespread New World species *H. courbaril* L., its spectral pattern is most similar to the African *H. verrucosa* Gaertn. In the pteridophytes there are an estimated 114 species showing relationships between Africa/Madagascar and the Neotropics of which 27 are common to both areas and 87 are species pairs. Migration seems to have been primarily from South America to Africa, but, as the authors note (Moran & Smith, 2001; Smith, pers. comm., 2004), the direction of movement is not always clear, and extinctions may have obscured the pattern. In a study of 123 species of *Elaphoglossum* Schott ex J. Sm. (Elaphoglossaceae), Rouhan et al. (2004) concluded on the basis of molecular evidence that at least 21 long-distance

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dispersal events occurred between the African-Indian Ocean region and the Neotropics. Renner (2004) further lists 110 angiosperm genera with species on both sides of the tropical Atlantic Ocean.

The principal explanation for the origin of biotic affinities between Africa and the Americas at the level of family or ± distantly related genera is vicariance dating to the separation of the New and Old World continents in Jurassic and Cretaceous times (Nelson & Rosen, 1981; Wiley, 1988). For more recently evolved taxa, one option is direct overland migration available until about the middle Eocene (see below). After that time, long-distance dispersal (LLD: Cain et al., 2003; Renner & Givnish, 2004) becomes progressively more important for those capable of crossing significant marine barriers; for example, for the 14 polypodiaceous families (sensu lato) listed by Moran and Smith (2001) as appearing primarily in the Tertiary.

In the earlier days of biogeography, long-distance transport essentially constituted a non-theory because it was invoked to explain how any organism could get anywhere given enough time. This was countered by the equally fatuous view that vicariance was *the* means of dispersion, and that dispersal biogeography was "a science of the improbable, the rare, the mysterious, and the miraculous" (Nelson, 1978). As noted elsewhere, vicariance, as thus proclaimed, has certain mystic qualities of its own (Graham, 1999: 318). More balanced hypotheses tailored to the age, morphological features, and systematic relationships of individual lineages have been proposed (Givnish & Renner, 2004) within a context of temporally better-defined tectonic events and climatic conditions (Graham, 2003a, b; present symposium).

It is also increasingly recognized that patterns of biotic affinities are immensely complicated, and that their origin is not likely resolvable by single-factor explanations. The most satisfactory models will be based on a systems approach, wherein a broad spectrum of factors varying in kind and degree, and in different combinations over time, form the basis for models accounting for the presence of identical or closely related organisms in distant geographic regions. The requisite information includes: (1) a taxonomy that accurately reflects real affinities and the level of relationship; (2) a knowledge of the dispersal processes (Higgins et al., 2003); (3) the principal transporting vectors (directional atmospheric and ocean currents, animal migration routes); (4) an adequate fossil record broadly establishing the probable time, place, and migration history of the lineage; (5) a knowledge of the relevant geologic events and landscape configurations during the existance of the lineage; and (6) a knowledge of the climates and climatic change, at the relevant times, across the area being transgressed. The North Atlantic land bridge became progressively discontinuous from the south (the Thulean route) to the north (the Svalbard route) after about the middle Eocene (Tiffney, 1985; Graham, 1999: 61–64), and this was at about the same time that global climates at the high latitudes were trending from the generally tropical hothouse interval of the Paleogene toward the temperate icehouse conditions of the Neogene. The Panama land bridge connecting North and South America was discontinuous until ~3.5 Ma (Ma = million years, millions of years ago), continuous but with lowland habitats suitable for tropical elements until ~2.5 Ma (Coates, 1997), and continuous with scattered upland habitats available for more temperate elements after that time (Graham, 1992; Burnham & Graham, 1999). Thus, the relevancy of these routes to a particular lineage depends on when the migration took place and the ecological requirements of the migrants. It is obvious that much of the information necessary for documenting migration routes and the origin of disjunct distributions is unknown for most organisms, for most places, for most of geologic time. Consequently, information that increases the range of feasible dispersal opportunities is useful in building a database commensurate with the complexity of the problem.

An observation particularly apparent in the satellite era is that large amounts of dust, bacteria, diatoms, phytoliths, fungi, spores, and probably lichen fragments are blown into the Caribbean region each year via the northeast and southeast trade winds from the Sahara Desert and the Sahel, the drought-plagued region south of the Sahara in Africa (BioBriefs, 1991; Reid et al., 1996; Cadée, 1998; Arimoto, 2001; Harrison et al., 2001; Kohfeld & Harrison, 2001; Prospero, 2001; Prospero & Lamb, 2003; Ryan, 2001; Griffin et al., 2002; Garrison et al., 2003; Toon, 2003). The amounts are impressive—13 million tons/yr. (Griffin et al., 2002), depositing one pound of phosphate/yr./acre into the Amazon Basin. The phenomenon has been recognized since the time of Darwin, who complained that it was "dirtying everything on board [the Beagle] and even hurting people's eyes" (Cadée, 1998: 16). Studies on the atmospheric transport of dust are primarily concerned with the climatic effects, the bleaching of corals, the spread of pathogens, and human health, but the potential for disseminating small propagules is obvious, if remote under present conditions.

However, conditions change, and another observation is that possibly the frequency (Trenberth, 2005) and certainly the intensity of hurricanes in the Atlantic Ocean and elsewhere has increased in recent decades (Moreno et al., 2002; Otvos, 2002; Emanuel,

2005). There has been an estimated two-fold increase in the number of hurricanes over the past six years compared to the previous 24 years, and the number of major hurricanes has increased 2.5 times (Bengtsson, 2001; Goldenberg et al., 2001; Hoyos et al., 2006; Webster et al., 2005). The suspected cause is global warming (Knutson et al., 1998; Goldenberg et al., 2001), and the change has been induced by an estimated global rise of only 0.6°C for the past century and 0.2°C–0.3°C in the last 40 years. An association not widely noted in the current literature is that this brings the observation on modern hurricanes into the realm of paleontological interest, because throughout the Tertiary temperatures were generally warmer than at present (see global paleotemperature curve; e.g., Graham, 1999: 89), and there have been times in the geologic past when they were much warmer than at present.

After the asteroid impact at the end of the Cretaceous Period 65 Ma, climates began to warm and reached a threshold between the early Paleocene (65 Ma) and the early Eocene (45 Ma) termed the LPTM (late Paleocene thermal maximum) and EECL (early Eocene climatic optimum), when temperatures were as high or higher than at anytime in the Phanerozoic Era (Pomerol & Premoli-Silva, 1986; Prothero, 1994; Huber et al., 2000; Schmitz et al., 2000). There was a rise in the early Miocene and extending into the middle Miocene (23–12 Ma with a peak at 18–14 Ma), and in the Middle Pliocene (3–4 Ma; Wrenn et al., 1999). The temperature values were ~12°C–15°C, 4°C–8 C, and 3°C–4°C warmer than at present, respectively, in the high latitudes (Graham, 1999: 89), and these periods of unusual warmth probably extended somewhat later in the mid-latitudes. If global warming is part of the cause for the modern rise in global temperatures, then warmer times of the past, and particularly these exceptionally warm intervals, should have witnessed an enhanced flow of directional winds and ocean currents between Africa and the Caribbean region, depending on the altered continental configurations (mostly in the Eocene) and the distribution of high and low pressure systems.

Two other observations are relevant to the kinds and amount of biological debris arriving from Africa during past warmer times, and especially during peaks of warmth. One is that at the time of the LPTM and EECL, the distance between Africa and the South America/Caribbean region was one-half to two-thirds that of the present. Intervening land may have been available along the mid-Atlantic Ridge, or above hot spots as at present on the Tristan da Cunha Group (oldest of the present islands is Nightingale Island at ~18 Ma fide www.btinternet.com) in the path of the opposite-flowing westerlies from South America to Africa. The other is that it was in the Eocene that the Greater Antilles began their principal period of emergence (Graham, 2003a, b), providing increased target areas for new arrivals.

There is considerable information available from projects such as PRIDE (Puerto Rico Dust Experiment) on the chemical composition, source, and configuration of dust particles being transported under present conditions, and these particles average 30μ–40μ in size (Colarco et al., 2003; Maring et al., 2003; E. Reid et al., 2003; J. Reid et al., 2003; R. Reid et al., 1996; Prospero et al., 2005). However, the maximum size and density of particles recovered is not tabulated, although it is probably about 100μ (or less fide Prospero, pers. comm., 2004). Silica minerals greater than 75μ have been found in the atmosphere and in water columns transported from eastern Asia across the Pacific Ocean (Betzer et al., 1988). These minerals and mineral aggregates are far heavier than the less dense and often more aerodynamically suited biological material, and it may be speculated that biological debris to a maximum size of 300μ–500μ is occasionally transported under present conditions (and rarely even larger material; see Renner, 2004: S31); probably larger material arrives under hurricane conditions (perhaps as much as 500μ–700μ); and still larger material was likely transported more frequently during times of maximum warmth and greater wind velocities in the LPTM and EECL (65–45 Ma), the early to middle Miocene (23–12 Ma), and the middle Pliocene (3–4 Ma; ?700μ–1200μ). Obviously, additional information is needed on the nature and maximum size and density of material presently being transported, as well as comparable data on relevant modern dissemules, especially during times of maximum wind velocity.

The point is that, collectively, these factors in the geologic past afforded greater possibilities for the introduction of a broader array of plants from Africa into the Caribbean region, possibly in the opposite direction at lower latitudes, across the Pacific Ocean, between Patagonia and Antarctica and beyond (Iriondo, 2000; Muñoz et al., 2004), and perhaps in other parts of the world, via wind, water, and drift than would seem plausible under modern conditions. As taxonomic relationships become better defined, the number of organisms recognized with African-New World affinities will likely increase, and the above observations of enhanced hurricane intensity, shorter distances, and increasing target areas should be considered in developing multi-faceted models to explain the introduction of some of them. This is particularly true for those with means of long-distance dispersal (Givnish & Renner, 2004), such as pieces of lichen, the spores of bryophytes and ferns, vegetative

reproductive fragments, and flowering plants with minute, plumose, and/or floating seeds such as in the Bromeliaceae (Givnish et al., 2004), *Ginorea* (Lythraceae; S. Graham, 2002), some Myrtaceae (Sytsma et al., 2004), Orchidaceae, Piperaceae, and others. Fossil and/or molecular evidence also suggests correspondence between times of introduction and the exceptional warm intervals of the Tertiary Period centered around 65–45 Ma, 23–12 Ma, and 3–4 Ma. In addition to some Melastomataceae and Lemnaceae (*Wolffiella* Hegelm.) estimated to have dispersed between Africa and South America 10–11 Ma (Renner, 2004, table 2), Tremetsberger (pers. comm., 2004) provides the following examples of plants with Old World–New World relationships, and estimates of the time of separation corresponding to ~3–4 Ma:

> Evidence for long distance dispersal across the Atlantic Ocean has been documented in *Senecio* sect. *Senecio* L. (Asteraceae; two inferred dispersals from the Old to the New World; Coleman et al., 2003). The Mediterranean and southern African floras were not distinguishable as sources of the main New World lineage, estimated to have become established during the middle Pliocene (3–4 Ma; Coleman et al., 2003).
>
> Käss and Wink (1997) hypothesized long distance dispersal of Old World (Mediterranean and African) lupines (Fabaceae) to the eastern parts of South America ("Atlantic region") and, independently, to North America and western regions of South America during the end of the Miocene (~8 Ma for dispersal to eastern parts of South America) and Pliocene (~3–4 Ma for dispersal to North America and western regions of South America).
>
> *Hypochaeris* L. (Asteraceae, Chichorieae) has about 15 species in the Old World, including Morocco, and more than 40 species in South America (Tremetsberger et al., 2004). DNA sequencing suggests a NW African origin for the South American group with long distance dispersal across the Atlantic Ocean. Based on molecular clock evidence, the trans-Atlantic dispersal from Morocco to South America can be estimated to have taken place ~3.5 Ma or less; i.e., during Pliocene or Pleistocene times (Tremetsberger et al., 2005).

Among other examples, Davis et al. (2004) suggest that in the Malpighiaceae, six amphi-Atlantic disjunctions occurred from South America to Africa between 60–31 Ma (middle Paleocene to early Oligocene) and at about 17 Ma (early Miocene). Divergence of neotropical and African *Symphonia* L.f. is placed at 17.36 ± 1.53 Ma (Dick et al., 2003). As the list increases it is worthwhile to monitor the examples for estimated times of dispersal, correspondence with warm intervals of the geologic past, and the distribution potential of the propagules, to determine if significantly increased directional winds and currents might be a factor in those patterns difficult to explain by vicariance or gradual overland migration alone.

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DISPERSAL-VICARIANCE ANALYSES IN THE TRIBE SINNINGIEAE (GESNERIACEAE): A CLUE TO UNDERSTANDING BIOGEOGRAPHICAL HISTORY OF THE BRAZILIAN ATLANTIC FOREST[1]

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Abstract

The historical biogeography of the tribe Sinningieae (Gesneriaceae) was analyzed based on distribution data and a molecular species-level phylogeny of 76 species. This plant group is distributed from Mexico to northern Argentina, but by far the highest diversity occurs within the Brazilian Atlantic forest. The dispersal-vicariance analysis method and a cladistic approach were used to infer ancestral areas as well as patterns of dispersal and vicariance. Results indicate that the Sinningieae probably arose in the coastal rain forest or in the neighboring tropical area delimited by the São Francisco river in Brazil. The majority of the dispersal-vicariance episodes were reconstructed between the Brazilian Atlantic rain forests and their neighboring inland areas (i.e., Paraná and São Francisco regions). In contrast, few dispersal-vicariance events were reconstructed between the tropical and subtropical areas of the Atlantic rain forest and between the Paraná and São Francisco regions. These results, together with ancestral areas inferred at the root of the main lineages, indicate an early north-south disjunction in Sinningieae. Occurrence of Sinningieae species in other areas, such as the Andes, the cerrado, Amazonia, northern South America, and Central America, are mainly explained by independent range expansions of single species from either the Paraná or the São Francisco regions. According to the dispersal-vicariance optimization, 20% of the speciation events are subsequent to inter-area dispersal and range expansion, 23% are associated with inter-area vicariance, and 57% occurred at a lower geographical scale within a single biogeographic area. These results pinpoint the need for a phylogenetic framework to correctly understand area relationships and the relative contribution of dispersal and vicariance events in present-day distribution patterns.

Key words: Atlantic forest, Brazil, dispersal, historical biogeography, Mata Atlântica, semi-deciduous forest, speciation, tropical rain forest, vicariance.

Resumen

Se analizó la biogeografía histórica de la tribu Sinningieae (Gesneriaceae) sobre la base de datos de la distribución y filogenia molecular al nivel de especie de 76 especies. Este grupo de plantas se distribuye desde México hasta el norte de Argentina, pero la diversidad más alta se encuentra en el bosque atlántico brasileño. Se usaron el método de análisis de dispersión-vicarianza y un acercamiento cladístico para inferir las áreas ancestrales así como los patrones de dispersión y vicarianza. Los resultados indican que las Sinningieae surgieron probablemente en el bosque húmedo tropical costero o en el área tropical vecina delimitada por el río São Francisco en Brasil. Se reconstruyeron la mayoría de los episodios de dispersión-vicarianza entre el bosque húmedo atlántico brasileño y sus áreas interiores vecinas (i.e., regiones de Paraná y de São Francisco). En contraste, se reconstruyeron pocos eventos de dispersión-vicarianza entre las áreas tropicales y subtropicales del bosque húmedo atlántico y entre las regiones de Paraná y de São Francisco. Estos resultados, junto con las áreas ancestrales inferidas en la raíz de los linajes principales, indican una temprana disyunción norte-sur en Sinningieae. La presencia de especies de Sinningieae en otras áreas tales como los Andes, los cerrados, la Amazonia, el norte de América del Sur y América Central se explica principalmente por expansiones independientes de la distribución de especies individuales sea desde la región de Paraná o de São Francisco. Según la optimización de la dispersión-vicarianza, el 20% de los acontecimientos de especiación es subsecuente a la dispersión inter-área y a la extensión de la distribución, el 23% se asocia con vicarianza inter-área, mientras que la mayoría de los eventos de especiación (el 57%) ocurrieron en una escala geográfica más baja dentro de una sola área biogeográfica. Estos resultados indican la necesidad de un marco filogenético para entender correctamente las relaciones del área y la contribución relativa de los eventos de dispersión y vicarianza en los actuales patrones de distribución.

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The Brazilian Atlantic forest is known for its high level of species diversity and endemism, as well as for being one of the most threatened tropical forests in the world (Mori et al., 1981; Terborgh, 1992; Morellato & Haddad, 2000; Myers et al., 2000). According to a broad definition, the Atlantic forest biome is composed of two types of vegetation. One is the coastal rain forest on the eastern slope of the mountain chain that runs along the coastline from southern to northeastern Brazil. The other is a neighboring semideciduous forest that extends farther inland in Brazil, with small portions entering Paraguay and Argentina (Fernandes & Bezerra, 1990; Spichiger et al., 1995; Morellato & Haddad, 2000). Despite recent efforts to characterize this biome (e.g., Oliveira-Filho & Fontes, 2000), little is known about its biogeographic history. Affinities among the different phytogeographic units that compose the Atlantic forest and their relationships with other areas in South America were generally based on floristic data, distribution patterns, or paleoenvironmental evidence (Smith, 1962; Harley, 1988; Prado & Gibbs, 1993; Oliveira-Filho & Ratter, 1995; Safford, 1999; Oliveira-Filho & Fontes, 2000; Pennington et al., 2000; Spichiger et al., 2004; Taylor & Zappi, 2004). Floristic studies indicate a strong link between the coastal Atlantic rain forests and the adjacent semideciduous forests (Oliveira-Filho & Fontes, 2000). On a larger scale, the semideciduous forests in Brazil and Paraguay were shown to be related with other fragments of tropical seasonal forest scattered along a large peri-Amazonian arc that passes through northeastern Brazil, the Paraguay-Paraná river basin, the Andes, and northern South America (Prado & Gibbs, 1993; Pennington et al., 2000). Other evidence based on distributions of closely related species indicates biotic exchanges between the Atlantic forest and either the Andes or the Guayana Highlands (Rambo, 1951; Smith, 1962; Granville, 1982; Safford, 1999; Prado, 2000). However, the place of origin or the direction and frequency of range movements are unknown for most taxonomic groups that occur in the Atlantic forest (cf. Berry et al., 2004; Sánchez-Baracaldo, 2004; Taylor & Zappi, 2004). It is also unclear how vicariance and dispersal have interacted to determine current distribution patterns. In this study, we investigate these issues in a tribe of Gesneriaceae using detailed distribution data and a nearly complete species-level phylogeny inferred from a simultaneous analysis of seven DNA regions (Perret et al., 2003).

The tribe Sinningieae includes three genera, *Paliavana* Vell. ex Vand., *Sinningia* Nees, and *Vanhouttea* Lem., and a total of 81 species (Clayberg, 1968; Wiehler, 1983, 1984; Chautems, 1990, 1991, 1995, 2002; Wiehler & Chautems, 1995; Chautems et al., 2000). Their habit varies from herbaceous plants with a perennial tuber in most *Sinningia* species to woody shrubs without tubers in *Paliavana* and *Vanhouttea*. They are mainly saxicolous, but some species are epiphytic or terrestrial (Chautems & Weber, 1999). Most of the Sinningieae taxa are found along mountain ranges (up to 2200 m) within the Brazilian Atlantic rain forest or in the adjacent areas occupied by seasonal vegetation types, i.e., the caatingas s.l. of eastern and northeastern Brazil (Prado, 2000), the cerrado biome in central Brazil, and the Misiones nucleus in the Paraguay-Paraná river basin (Prado & Gibbs, 1993). A restricted number of species (5) are also found farther along the Andes, in Amazonia, northern Colombia, Venezuela, the Guayana Highlands, Central America, and southern Mexico. The Sinningieae is therefore an appropriate group for investigating general patterns in historical biogeography of the Brazilian Atlantic forest and its relationships with other areas in South America.

The biogeographic history of the Sinningieae was reconstructed using a phylogenetic framework and methods, such as the dispersal-vicariance analysis that considers dispersal and extinction explicitly (Ronquist, 1997), and a cladistic approach that assumes no particular speciation mechanism (Bremer, 1992). Our goals are several: (1) to reconstruct the ancestral distribution of the tribe; (2) to infer directions and frequency of dispersal events, especially within the domain of the Atlantic forest and between this region and other biogeographic areas in South America; and (3) to evaluate how inter-area dispersal and vicariance processes have interacted during Sinningieae diversification.

Material and Methods

Sampling and Phylogenetic Analysis

Sixty-two species of *Sinningia*, six species of *Paliavana*, and eight species of *Vanhouttea* were included in the phylogenetic analysis. This sampling represents all currently recognized species in the tribe Sinningieae, with the exception of *Sinningia helleri* Nees, *S. schomburgkiana* (Kunth & Bouché) Chautems, and *S. sulcata* (Rusby) Wiehler, for which no material was available. The two selected outgroups, *Smithiantha laui* Wiehler and *Nematanthus villosus* (Hanst.) Wiehler, belong to the tribes Gloxinieae and Episcieae, respectively, and are closely related to Sinningieae based on a molecular phylogenetic analysis of the entire family (Smith et al., 1997). A full list of taxa with author attributions and vouchers is provided in Appendix 1.

The plastid DNA spacers *trn*T-*trn*L, *trn*L-*trn*F, *trn*S-*trn*G, *atp*B-*rbc*L, introns *trn*L and *rpl*16, together with a portion of the nuclear encoded *ncp*GS gene were sequenced following the procedure described in Perret et al. (2003). All sequences have been deposited in EMBL/GenBank (accessions AJ438352–AJ438434, AJ439249–AJ439331, AJ439745–AJ439829, AJ439900–AJ439984, AJ487702–AJ487786, AJ459606–AJ459691). Because these regions were found compatible (Perret et al., 2003), we performed a combined analysis with 5812 characters using PAUP*4.0b8 (Swofford, 1999). We made a 50% majority-rule bootstrap consensus tree from 1000 bootstrap replicates (Felsenstein, 1985) using maximum parsimony, tree bisection-reconnection swapping, simple addition of taxa (SIMPLE), and a limit of 500 trees retained at each replicate (MAXTREES = 500). This tree was then used as a constraint tree in a maximum likelihood analysis using the HKY85 model, incorporating rate variation across sites and proportion of invariable sites (Yang, 1996).

BIOGEOGRAPHIC DATA AND DELIMITATION OF AREAS

Distribution data were obtained for all 76 species of Sinningieae used in the phylogenetic analysis. Species distributions were based on over 3000 accessions from 67 international and Brazilian herbaria (i.e., ALCB, ASE, B, BH, BHCB, BOTU, CAY, CGE, CEN, CEPEC, CESJ, CONN, E, EAN, ESA, F, FCQ, FUEL, G, GB, GFJP, GUA, HAS, HBR, HEPH, HUEFS, IAC, IAN, IBGE, ICN, INPA, IPA, K, MBM, MBML, MG, MO, NA, NY, P, PACA, PEUFR, PKDC, PY, R, RB, RBR, RUSU, S, SEL, SP, SPF, SPSF, UB, UC, UEC, UFG, UFMT, UFP, UPCB, UPS, US, VEN, W, WIS, WU, Z). Part of this chorological information is available in various published floras and taxomomic treatments for Argentina (Toursarkissian, 1969), Paraguay (Chautems, 1993), and Brazil (Chautems, 1990, 1991, 1995, 2002, 2003a, 2003b; Woodgyer, 1995; Chautems et al., 2000; Araujo et al., 2005). Representative specimens for all species included in this study are listed in Appendix 2. Distribution maps were produced using the software ArcView GIS 3.2 (ESRI, 2000). The total range of Sinningieae in South and Central America was partitioned into 12 biogeographic areas (Fig. 1). These are: (1) the northern portion of the Brazilian Atlantic rain forests that lies north of the Tropic of Capricorn (A_N); (2) the southern portion of the Brazilian Atlantic rain forests that lies south of the Tropic of Capricorn (A_S); (3) the São Francisco region (F) (caatingas province s.l. according to Prado, 2000), including the semideciduous forests and the campos rupestre distributed east of the São Francisco river in Brazil and the caatingas of northeastern Brazil; (4) the Paraná region (P) (sensu Cabrera & Willink, 1973), including the semideciduous forest of the Paraguay-Paraná river system in eastern Paraguay, northeastern Argentina, and southwestern Mato Grosso do Sul (Misiones nucleus) and the Araucaria forest in southern Brazil; (5) the cerrado (C); (6) the Chaco (O); (7) the Pampas in southern Brazil and Uruguay (U); (8) the southern Andes (D_S); (9) the northern Andes (D_N); (10) Amazonia (Z); (11) northern Colombia-Venezuela and the Guayana Highlands (V); and (12) Central America and southern Mexico (M). We are aware that some areas are composed of distinct phytogeographic units that are usually considered separately.

ANCESTRAL AREA RECONSTRUCTION

Ancestral distributions were reconstructed on the phylogenetic tree using dispersal-vicariance analysis (DIVA; Ronquist, 1997), as implemented in the program DIVA 1.1 (Ronquist, 1996). This method is event-based and allows for the inference of the ancestral distribution in a given phylogeny without forcing vicariance events to conform to a hierarchical pattern. DIVA is thus appropriate to infer biogeographic patterns even when area relationships are reticulated (Sanmartín et al., 2001). The method searches for optimal reconstruction of ancestral distribution by assuming a vicariance process but incorporates the potential contribution of dispersal and extinction in shaping the current distributional pattern. The optimal solutions are those that minimize the number of dispersal and extinction events under a parsimony criterion. In our analysis, we limited the number of areas allowed for an ancestral distribution to a maximum of three, using the "maxareas" option. DIVA reconstructions were used to determine the direction of movement as well as to quantify the biogeographic processes such as dispersal, vicariance, and speciation within a single area.

In addition to DIVA, ancestral areas of the Sinningieae and of its major lineages were also determined using the method proposed by Bremer (1992). This approach is a cladistic procedure in which each area is treated as a single character that can be optimized on a cladogram. For a particular clade, one can calculate the necessary number of gains and losses of each area by using forward or reverse Camin-Sokal parsimony, respectively. The ratio between gains and losses provides an estimate of the likelihood that one particular area is part of the ancestral region. The area with the highest gain:loss ratio is considered to have 100% probability of being part of the ancestral region.

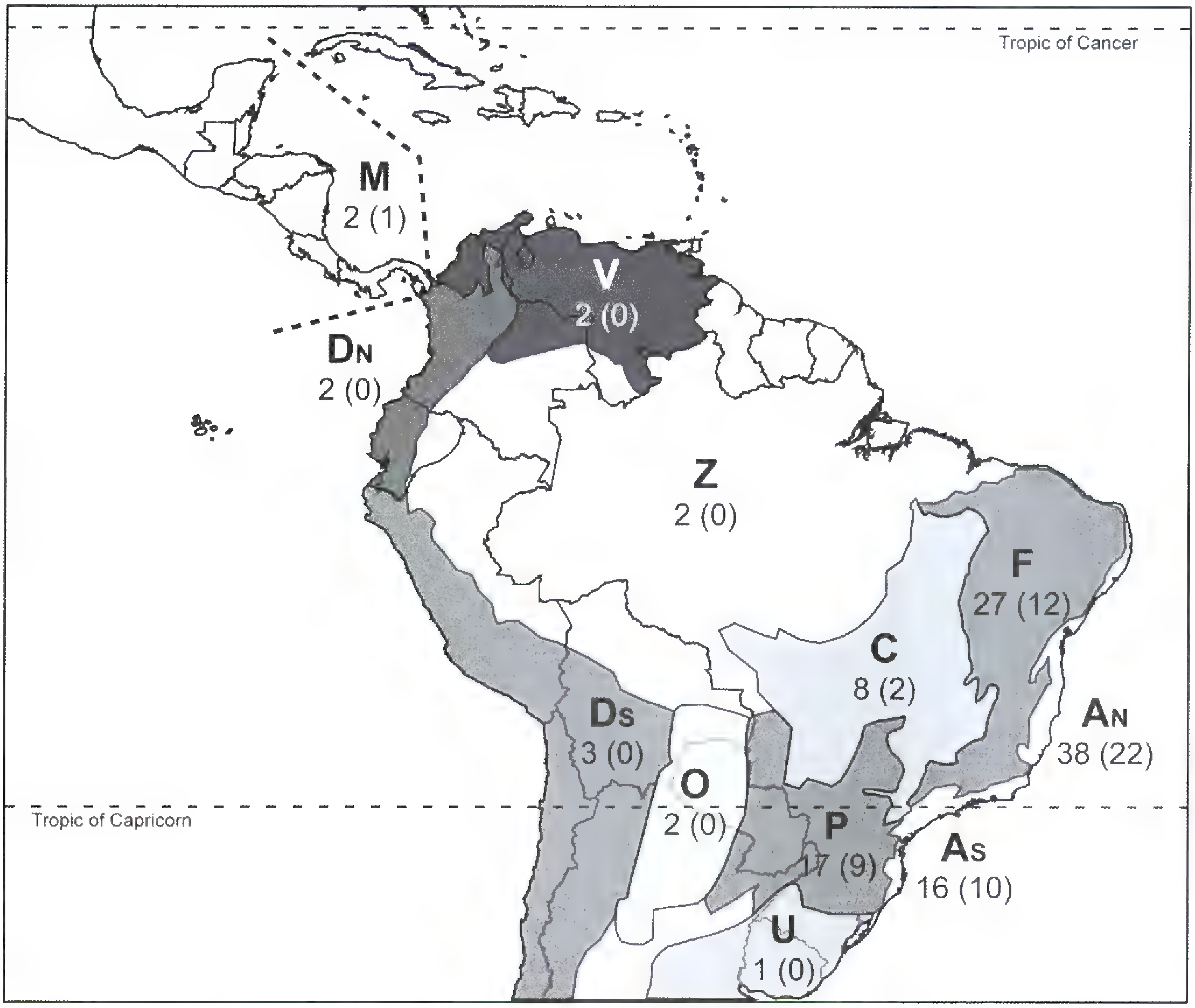

Figure 1. Biogeographic areas used to delimit Sinningieae species distributions in South and Central America. A_N, A_S = the northern and southern portions of the Brazilian Atlantic rain forests that lie respectively north and south of the Tropic of Capricorn; F = the São Francisco region; P = the Paraná region; C = the cerrado region; O = the Chaco; U = the Pampas in southern Brazil and Uruguay; D_S = southern Andes; D_N = northern Andes; Z = Amazonia; V = northern Colombia, Venezuela, and the Guayana Highlands; M = Central America and southern Mexico. Numbers indicate the total number of species occurring in each area. Numbers in parentheses indicate the number of species endemic to the area. Delimitations of areas were modified after Gentry (1982), IBGE (1993), and Pennington et al. (2000).

Results

Phylogenetic analyses

The phylogenetic tree resulting from the maximum likelihood analyses and the bootstrap supports (BS) based on maximum parsimony are shown in Figure 2. Tribe Sinningieae is monophyletic, but both genera *Vanhouttea* and *Paliavana* are polyphyletic and embedded in *Sinningia*. Taxa are distributed into three main clades named *Dircaea* (BS 100%), *Corytholoma* (BS 73%), and *Sinningia* (BS 64%), as well as into two smaller early-diverging clades named *Vanhouttea* (BS 100%) and *Thamnoligeria* (BS 73%). The tree used here is in full agreement with our previous complementary and comprehensive phylogenetic analyses (Perret et al., 2003).

Distribution patterns

The tribe Sinningieae shows a continental-wide distribution between southern Mexico and northern Argentina, but the highest species richness occurs within southeastern Brazil (Fig. 1). Out of 76 species analyzed, 33 (43%) are restricted to the Brazilian Atlantic rain forest. Within this area, species are located either in the tropical zone (22 species) or south of the Tropic of Capricorn (10 species), whereas only one species is distributed across both zones (Fig. 3). Species distributed farther inland are either restricted to the areas of São Francisco, the cerrado, and Paraná (totaling 23 species, 30%), or occur across the tropical portion of the Atlantic rain forest and the São Francisco region (10 species, 13%; Fig. 3). The remaining 10 species are widespread within Brazil or

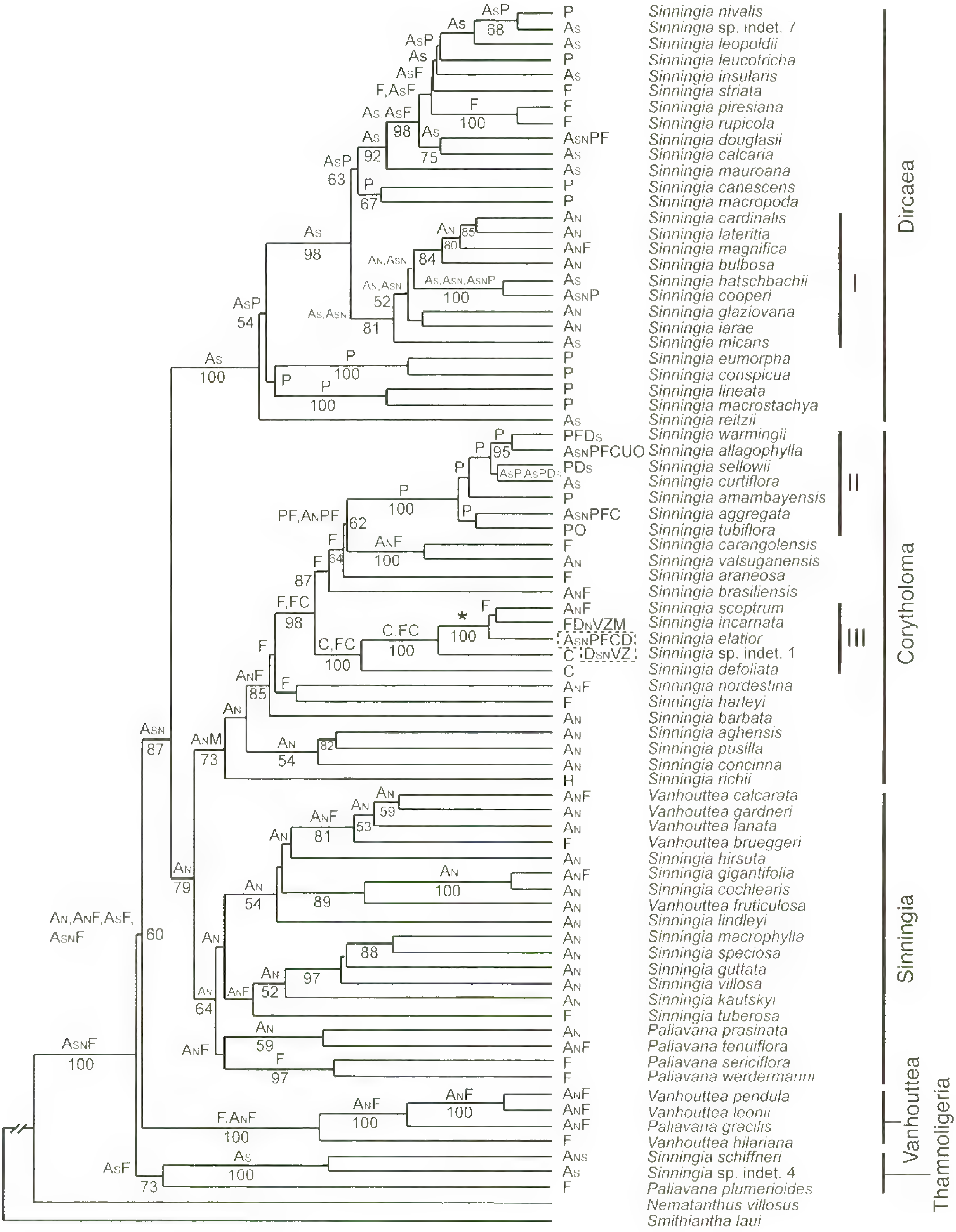

Figure 2. Phylogenetic hypothesis for the tribe Sinningieae used to reconstruct ancestral areas. The tree is based on a simultaneous analysis of plastid and nuclear DNA sequences (regions *trn*T-*trn*L, *trn*L-*trn*F, *trn*S-*trn*G, *atp*B-*rbc*L, *rpl*16, and *ncp*GS). Numbers below the branches are bootstrap proportions (only if ≥ 50%). Ancestral areas at each internal node were reconstructed using DIVA (Ronquist, 1997). Abbreviations for biogeographic areas are defined in Figure 1. The asterisk indicates ambiguous reconstruction of the ancestral area. Names of the five major clades are indicated, and the three subclades discussed in this study are identified with Roman numerals.

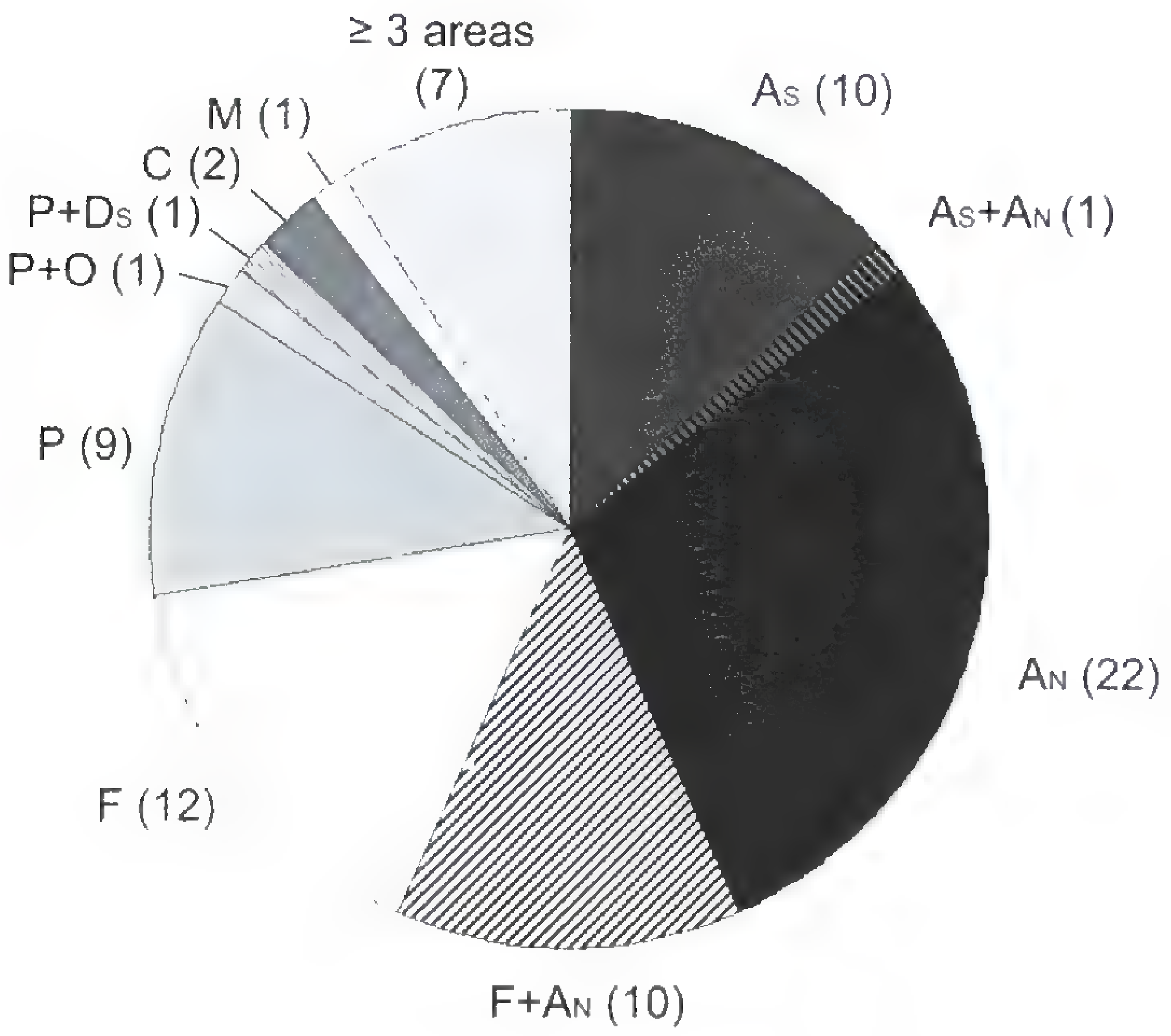

Figure 3. Pie chart summarizing the number of species according to their distributions: endemic to a single area, across two areas, or in a combination of at least three areas. Biogeographic areas are delineated and abbreviations are defined in Figure 1.

occur outside of the country in the Chaco (2), the Pampas (1), the Andes (3), Amazonia (2), northern South America (2), and Central America and southern Mexico (2, Fig. 1). Most of the latter species are distributed in a combination of more than two areas (Fig. 3).

Patterns of geographical distribution differ among the main lineages within Sinningieae (Fig. 4). The range of the clade *Corytholoma* (23 species) covers the full geographical extent of the tribe Sinningieae (Fig. 4A). In Brazil, species richness of *Corytholoma* is the highest north of the Tropic of Capricorn within the northern Atlantic rain forest and the São Francisco region. Occurrences outside of Brazil are due to a few species distributed in Paraguay and southern Argentina (*Sinningia aggregata* (Ker Gawl.) Wiehler, *S. allagophylla* (Mart.) Wiehler, *S. elatior* (Kunth) Chautems, *S. tubiflora* (Hook.) Fritsch, and *S. warmingii* (Hiern) Chautems), in the southern Andes (*S. elatior*, *S. sellowii* (Mart.) Wiehler, and *S. warmingii*), in the northern Andes (*S. elatior* and *S. incarnata* (Aubl.) D. L. Denham), in northern South America (*S. elatior* and *S. incarnate*), and in Central America up to southern Mexico (*S. incarnata* and *S. richii* Clayberg). All of these species are widespread and clustered in the subclades II and III within *Corytholoma* (Fig. 2), with the exception of the first diverging species of the clade, *S. richii*, which is a narrow endemic in the state of Veracruz in Mexico (Clayberg, 1968).

The clade *Sinningia* (19 species) is distributed from eastern to northeastern Brazil (Fig. 4B). The majority of these species (12) are restricted to the northern Atlantic rain forest, whereas the remaining seven are found in the adjacent São Francisco region along the Mantiqueira and Espinhaço mountain ranges.

The clade *Dircaea* (27 species) is distributed from southern to southeastern Brazil (Fig. 4C). Within this clade, 16 species have a range limited to the Atlantic rain forest, whereas the remaining 11 species are restricted to either the Paraná (8) or to the southern part of the São Francisco region (3). The species that extend the farthest from the Atlantic coast are *Sinningia macropoda* (Sprague) H. E. Moore, which reaches eastern Paraguay (Chautems, 1993), and *S. magnifica* (Otto & A. Dietr.) Wiehler, which is found along the "Cadeia do Espinhaço" in Minas Gerais (Araujo et al., 2005).

The two early-diverging clades *Vanhouttea* (4 species) and *Thamnoligeria* (3) are distributed in eastern Brazil (Fig. 4D). The species of the clade *Vanhouttea* occur at elevations usually between 1200 and 2200 m in a vegetation type locally called campos de altitude in the southern part of the São Francisco region along the mountain ranges of Mantiqueira, Espinhaço, and Caparaó. Distribution of the clade *Thamnoligeria* is more disjunct, including elements from the Atlantic rain forest (*Sinningia schiffneri* Fritsch and an undescribed species of *Sinningia*, *S.* sp. indet. 4) together with a mountainous species (*Paliavana plumerioides* Chautems), which occur in the central part of the "Cadeia do Espinhaço" (Chautems, 2002).

ANCESTRAL AREAS AND DISPERSAL PATTERNS IN BRAZIL

According to the DIVA optimization shown in Figure 2 and Bremer's method (Table 1), the ancestral area reconstructed at the root of the tribe Sinningieae most likely comprises the Atlantic rain forests together with the São Francisco region. The ancestral area of the clade *Dircaea* was restricted to the southern Atlantic rain forest, whereas the northern Atlantic region was probably part of the ancestral distribution of the clade grouping *Corytholoma* and *Sinningia* (Fig. 2 and Table 1). Subsequent to this early north-south disjunction, these two lineages followed different biogeographic pathways. In the clade *Dircaea*, dispersal-vicariance events occurred predominantly between the southern Atlantic rain forest and the Paraná region, whereas in the *Corytholoma* and *Sinningia* clades, dispersal-vicariance events were more frequent between the northern Atlantic rain forest and the São Francisco region (Table 2). Overall, 22 dispersal events were reconstructed between the coastal rain forest and the more seasonal vegetation of neighboring inland areas (i.e., Paraná and São Francisco; Fig. 5). Movements inland

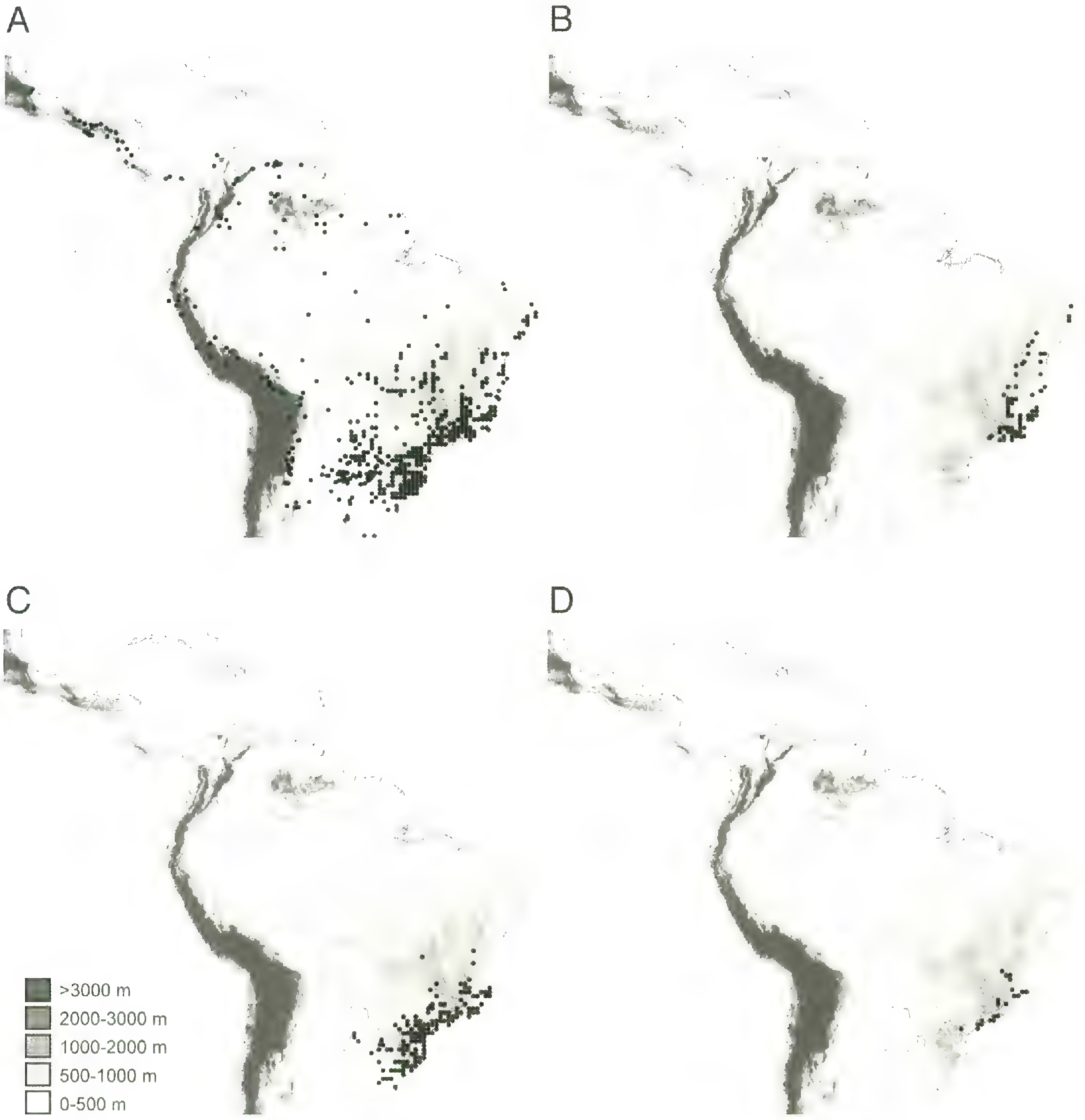

Figure 4. Distribution of the main clades within the Sinningieae as defined in Figure 2. —A. *Corytholoma* (23 species). —B. *Sinningia* (19 species). —C. *Dircaea* (27 species). —D. *Vanhouttea* and *Thamnoligeria* (7 species).

from the coast were more frequent than in the opposite direction (Fig. 5). In contrast, following a pattern parallel to the coast, only seven dispersal events were reconstructed between the northern and southern Atlantic rain forest and between the Paraná and the São Francisco regions (Fig. 5).

DISPERSAL PATTERNS AT A CONTINENTAL SCALE

Species found in the Chaco, the Pampas, the Andes, Amazonia, northern South America, and Central America are widespread and clustered in subclades II and III within the *Corytholoma* clade (Fig. 2, see below for an exception). Ancestral areas reconstructed at the root of subclades II and III indicate that expansions of these taxa outside of Brazil occurred from two distinct biogeographic units: the Paraná and São Francisco + cerrado, respectively (Figs. 2 and 5). Such dispersal events were optimized on terminal or nearly terminal branches, indicating that they most likely are recent and concern mainly individual taxa (Fig. 2). The tie between the Paraná region and the Andean piedmont in the southern Andes is indicated by the distribution of *Sinningia sellowii* (Fig. 6B) and *S. warmingii* (Fig. 6A). The link between the São Francisco region and the Andes through the cerrado is indicated by the range of *S. elatior* (Fig. 6C), which also spreads into Amazonia and northern Colombia and Venezuela. In addition to these Brazilian–southern Andean connections, a tie between eastern

Table 1. Ancestral area reconstruction based on Bremer's (1992) method for the Sinningieae and its main clades defined in Figure 2. Ancestral area scores (AA) are probabilities that a given area is part of the ancestral area for the clade. G = number of necessary gains under forward Camin-Sokal parsimony; L = number of necessary losses under reverse Camin-Sokal parsimony; AA = G/L quotients rescaled to a maximum value of 1 by dividing with the largest G/L value. Abbreviations for biogeographic regions are defined in Figure 1.

Areas	G	L	G/L	AA
Sinningieae				
A_N	21	25	0.84	1
F	20	31	0.66	0.77
A_S	13	25	0.52	0.62
P	11	26	0.42	0.50
C	7	18	0.39	0.46
D_N + V + Z + M	3	11	0.27	0.32
D_S	3	18	0.17	0.20
Dircaea				
A_S	8	8	1	1
A_N	4	8	0.5	0.5
P	6	12	0.5	0.5
F	4	11	0.36	0.36
Corytholoma + *Sinningia*				
A_N	15	14	1.07	1
F	13	18	0.72	0.67
C	6	14	0.43	0.4
P	5	12	0.42	0.39
D_N + V + Z + M	3	8	0.37	0.35
A_S	4	15	0.27	0.25
D_S	3	15	0.2	0.19

Brazil and the Guayana Shield region through Amazonia can be also hypothesized based on the current distribution of the sister species *S. sceptrum* (Mart.) Wiehler and *S. incarnata* (Fig. 6D). According to the ancestral area reconstruction, the range of *S. incarnata* expanded in a northwestern direction from the São Francisco region (Figs. 2 and 5). Finally, we cannot exclude an ancient colonization event through Central America according to the basal position of *S. richii* within *Corytholoma* and its occurrence in the state of Veracruz in Mexico (Figs. 2 and 5).

RELATIVE IMPORTANCE OF DISPERSAL AND VICARIANCE

In Sinningieae, DIVA analysis identified a total of 49 inter-area dispersal events, among which 15 are reconstructed on internal branches. Because there are 75 internal nodes in the phylogenetic tree of the Sinningieae, this means that 20% of the speciation events were preceded by range expansion. The total number of vicariance events is 17 (23%), whereas the remaining 43 speciation events (57%) occurred within a single area.

Table 2. Number of vicariance and dispersal events among areas within the Brazilian Atlantic forests reconstructed for the Sinningieae main clades (inferred from the DIVA analysis in Figure 2). Values in parentheses indicate the number of dispersal events reconstructed on internal branches only. Abbreviations for biogeographic regions are defined in Figure 1.

	Clades		
Events	*Dircaeae*	*Corytholoma*	*Sinningia*
Vicarance between:			
A_N – F	0	2	3
A_S – P	4	0	0
A_N – P	0	0	0
A_S – F	1	0	0
A_N – A_S	0	0	0
F – P	0	1	0
Dispersal between:			
$A_N \leftrightarrow$ F	1 (0)	4 (3)	6 (3)
$A_S \leftrightarrow$ P	5 (4)	3 (1)	0
$A_N \leftrightarrow$ P	1 (0)	2 (0)	0
$A_S \leftrightarrow$ F	1 (1)	0	0
$A_N \leftrightarrow A_S$	2 (1)	0	0
F $\leftrightarrow$ P	0	3 (1)	0

Out of the 15 dispersals reconstructed on internal branches, 12 (16% of the speciation events) correspond to range extensions of rain forest lineages into more seasonal areas of the Paraná or São Francisco regions. All of these events were immediately followed by vicariance that further split the combined area into its constituents. These dispersal-vicariance episodes were reconstructed on deep branches within the main lineages as well as on branches closer to the tips (Fig. 2).

Discussion

ANCESTRAL AREA AND DISPERSAL PATTERNS IN BRAZIL

Dispersal-vicariance reconstruction and results of Bremer's method indicate that the Brazilian coastal Atlantic rain forest and the adjacent São Franciso region are the likely ancestral areas of the tribe Sinningieae. Other plant groups that are reported to have diversified in the Brazilian Atlantic regions include *Nematanthus* Schrad. (Gesneriaceae; Chautems, 1988), *Fuchsia* L. sect. *Quelusia* Vand. (Onagraceae; Berry, 1989; Berry et al., 2004), *Cattleya* Lindl. alliance (Orchidaceae; van den Berg & Martins, 1998; van den Berg et al., 2000), *Aechmea* Ruiz & Pav. (Bromeliaceae; Faria et al., 2004), herbaceous Bambusoideae (Soderstrom & Calderon, 1974), and several genera within the Cactaceae (Taylor & Zappi, 2004). We hope that the increasing

body of monographic works and species-level phylogenetic analyses will soon provide opportunities to evaluate the biogeographic significance of our results in relation to other taxonomic groups.

Within the three major clades, *Dircaea*, *Corytholoma*, and *Sinningia*, several independent dispersals between the Brazilian Atlantic rain forest and adjacent inland areas of the Paraná and São Francisco regions were reconstructed. These floristic exchanges are consistent with the floristic similarities found between rain forests and semideciduous forests enclosed in the Brazilian Atlantic region (Oliveira-Filho & Fontes, 2000). It is worth noting that migrations were more frequent from the rain forest to neighboring areas than in the opposite direction (Fig. 5). Therefore, the coastal rain forest could constitute the predominant source of Sinningieae evolution in the more seasonal adjacent regions. According to Oliveira-Filho and Fontes (2000: 808), "the tree flora of semideciduous forests is a fraction of the much richer rain forest flora, and probably is composed of species able to cope with relatively longer dry seasons." Similarly, in Sinningieae, the repeated range extensions into the semideciduous forests most likely are correlated with independent evolution of lineages that are more tolerant to rainfall seasonality.

Dispersal patterns between coastal and adjacent inland areas differ among lineages. In the sister clades *Corytholoma* and *Sinningia*, dispersal events occurred mainly between the northern portion of the Atlantic rain forest and the São Francisco region (Table 2). These dispersal events, as well as the fact that a large number of taxa are distributed in both areas, conform to the relative gradual floristic and climatic gradient that exists from the Atlantic coast to the interior above the Tropic of Capricorn (Oliveira-Filho & Fontes, 2000). In *Dircaea*, dispersal events were mainly reconstructed between the southern portion of the coastal rain forest and the Paraná region. Dispersals along this route were also hypothesized for elements within the plant families Myrtaceae and Palmaceae, as well as for various groups of vertebrates (Mueller, 1973; Cracraft, 1985; Spichiger et al., 1995). These taxa were considered to be expansive rain forest elements because they are well represented in the Atlantic rain forest and also penetrate into the meridional Planalto region and eastern Paraguay. In these cases, the coastal mountain range Serra do Mar does not act as a hermetic barrier, despite its role in creating a sharp transition between subtropical and typical seasonal conditions (Oliveira-Filho & Fontes, 2000).

The ancestral areas reconstructed at the root of the main lineages *Dircaea* and *Corytholoma* + *Sinningia* support an early north-south disjunction between the subtropical and the tropical portions of the Atlantic forests (Fig. 2). The paucity of subsequent exchanges between northern and southern coastal regions and between the São Francisco and Paraná regions indicates that isolation of these lineages largely persisted during their diversification. Only two noticeable exceptions were reconstructed on internal branches. One is the northward shift of subclade I along the coast (cf. Fig. 2); the other involves colonization of the Paraná region from the São Francisco region by the widespread subclade II (Fig. 2). The relatively low frequency of dispersals along a northeast-southwest axis conforms to the strong floristic differentiation found between northern and southern blocks of Atlantic forests (Oliveira-Filho & Ratter, 1995; Oliveira-Filho & Fontes, 2000) and to the latitudinal divisions of the coastal rain forest into different centers of endemism (Mueller, 1973; Brown, 1987; Prance, 1987). Similarly, at the populations level, recent studies on the genetic differentiation of the Brazilian Cherry (*Eugenia uniflora* L.) along the Atlantic rain forest support the hypothesis that a past barrier obstructed gene flow between southern Brazil and the rest of the country (Salgueiro et al., 2004). Factors proposed to explain the relative isolation of tropical and subtropical areas of Brazil include mean temperature gradient along the coast (Oliveira-Filho & Fontes, 2000), contrasting vegetation history on each side of the Tropic of Capricorn during the Quaternary (Brown, 1987; Behling & Negrelle, 2001), and the barrier effect of the dry climate and unforested landscape that locally persisted in the region of Cabo Frio in the state of Rio de Janeiro (Mueller, 1973). In Sinningieae, these factors may have contributed to prevent *Sinningia* and *Corytholoma* from moving south or *Dircaea* from moving north.

DISPERSAL PATTERNS AT A CONTINENTAL SCALE

Occurrence of Sinningeae outside of Brazil in the Andes, Amazonia, northern South America, or beyond into Central America and southern Mexico most likely is explained by several independent range expansions of single species embedded within the *Corytholoma* clade. The analyses of these biogeographic events and present-day species distribution provide an opportunity to infer the pathways along which these areas were colonized.

The four Sinningieae species extending their range in the Andes are also found in the Paraná region, the São Francisco region, or in both regions (Fig. 6). Without exception, these widespread species are clustered in subclades II and III within *Corytholoma*

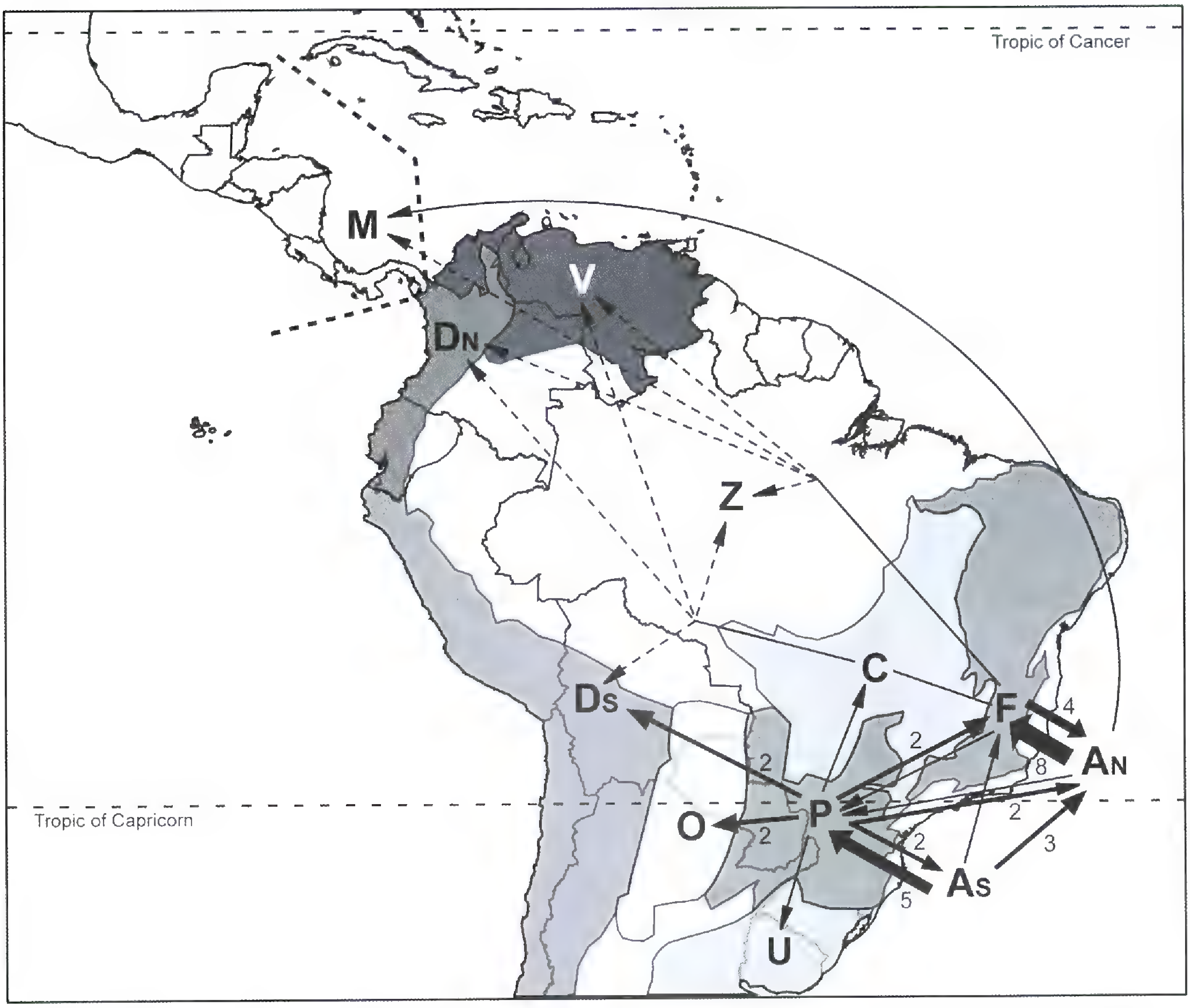

Figure 5. Direction and number of dispersal events between biogeographic areas of South and Central America in the Sinningieae (inferred from the DIVA analysis on Figure 2). The thickness of the arrows is proportional to the frequency of the dispersal events. Number of dispersal events is indicated when greater than 1. Dotted arrows indicate range expansion in several biogeographic areas reconstructed on a single branch of the phylogenetic tree (in subclade III, Fig. 2). Abbreviations for biogeographic areas are defined in Figure 1.

(Fig. 2). Distribution of these species in areas occupied by tropical seasonal forest, such as the Misiones nucleus, the Andean piedmont, and the eastern foothills and intermontane valleys of the Andes, fit with the Pleistocene arc distribution pattern described by Prado and Gibbs (1993). These data and recent distribution maps available for the Cactaceae indicate that this pattern may concern a larger number of taxa than had been initially thought (Taylor & Zappi, 2004). Direction and frequency of dispersal events between the Brazilian Atlantic regions and the Andes have rarely been tested using molecular phylogenies. However, the few existing studies have already indicated that the direction of such dispersal events may differ according to the taxonomic group considered (Voelker, 1999; Berry et al., 2004; Sánchez-Baracaldo, 2004; Taylor & Zappi, 2004). In Sinningieae, dispersal-vicariance analyses support three independent migrations into the southern Andes along two distinct biogeographic pathways (Fig. 5). In subclade II, colonization of the Paraná basin predated the independent dispersions of *Sinningia warmingii* and *S. sellowii* into the southern Andes (Fig. 2). The distribution of these species suggests the existence of a narrow bridge between the Paraná basin and the sub-Andean piedmont through the northern extremity of the Chaco in Paraguay and southeastern Bolivia (Fig. 6A, B). This strip of land has already been identified as a crucial connecting area for several woody elements that are found both in the Paraná and the Andean piedmont areas but that are missing in the xeromorphic Chaquean vegetation (Prado, 2000; Spichiger et al., 2004). A second dispersion route is indicated by *S. elatior*, linking the São Francisco region with the eastern foothills of the Andes through the cerrado, the Pantanal, and Bolivia (Fig. 6C). This species occurs mostly in grasslands on marshy grounds at altitudes not exceeding 1200 m. Ancestral

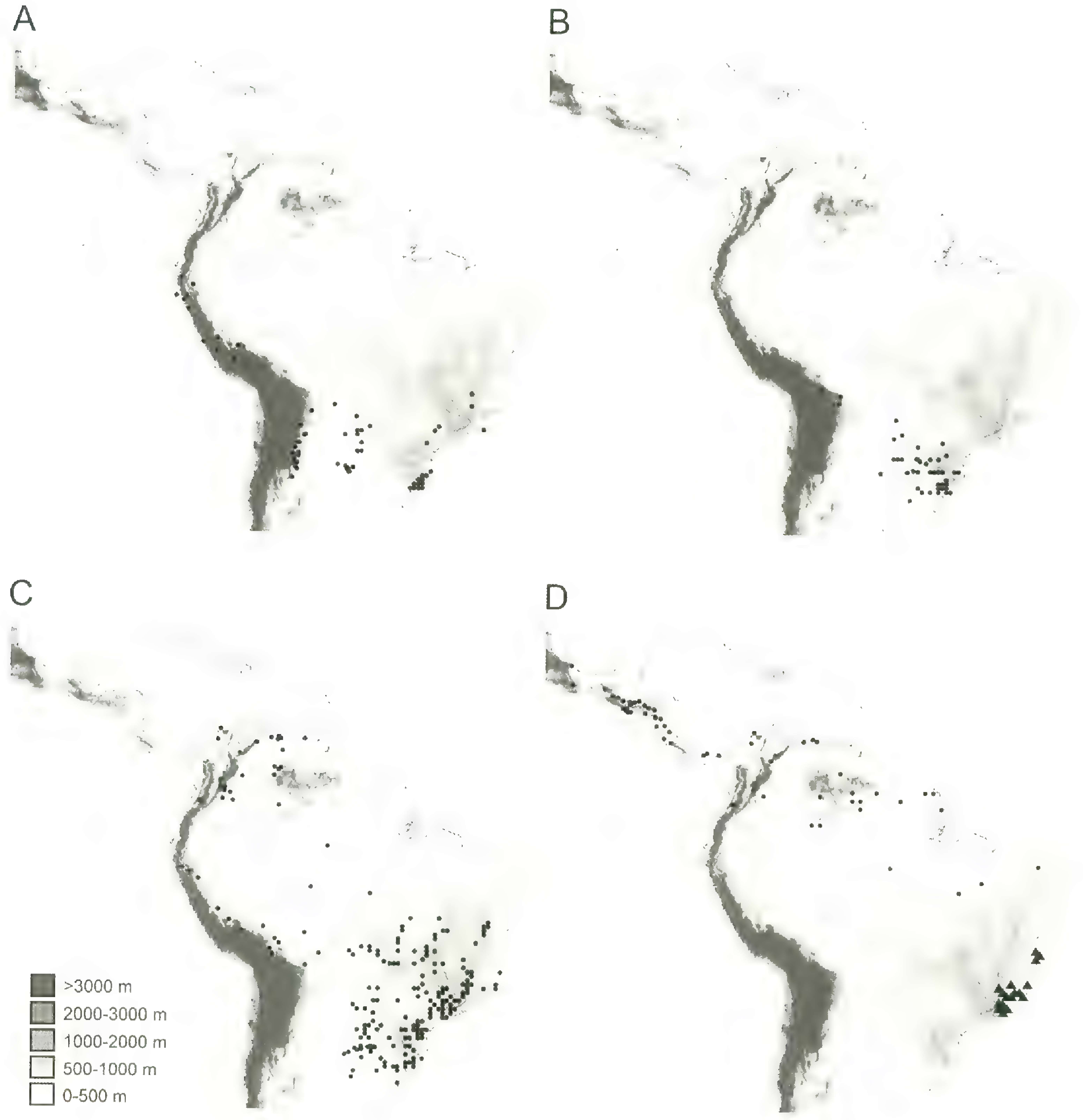

Figure 6. Distributions of widespread species showing a connection between Brazil, the Andes, and/or other regions in northern South America, Central America, and southern Mexico. —A. *Sinningia warmingii*. —B. *S. sellowii*. —C. *S. elatior*. —D. *S. incarnata* (solid circle) and *S. sceptrum* (solid triangle).

area reconstructions within subclade III indicate that expansion of *S. elatior* (or its close ancestors) into non-Brazilian areas occurred from the cerrado and/or the São Francisco region (Figs. 2 and 5). The westward extensions of *S. elatior* follow the northern migration track described by Prado (2000) for elements of the seasonal tropical dry forest that cross the cerrado following a net of gallery forest along a northeast-southwest arc (Oliveira-Filho & Ratter, 1995). Occurrence of *S. elatior* further north in South America most likely is explained by northward dispersal along the Andes, although the few specimens collected in the Brazilian states of Pará and Amazonas may also support a migration route through the Amazon basin.

Dispersal patterns of these three widespread species are consistent with the hypothesis about historical plant migration routes involving dry seasonal forest formations (Pennington et al., 2000; Spichiger et al., 2004). Hence, dispersion of these Sinningieae species along the Andes from either the Paraná or the São Francisco regions could have been promoted by the extension of these formations, which may have taken place during the drier and cooler periods of the Pleistocene (Pennington et al., 2000). However, a careful test of this hypothesis would

require a calibration of the phylogenetic tree to estimate the absolute timing of such dispersal events. So far, such an attempt led to ambiguous results because of the lack of dated fossils or pollen records for the Sinningieae.

In addition to migrations along the Pleistocene arc, the sister relationship between *Sinningia incarnata* and *S. sceptrum* provides evidence for a link between the Guayana Shield region and eastern Brazil (Fig. 6D). The few known ocurrences of *S. incarnata* within Amazonia in the Brazilian states of Maranhão, Pará, Amazonas, and Roraima may indicate the route followed by this species during its northwestern expansion into northern South America and beyond. Similarly, geographic disjunction between eastern Brazil and the Guayana Shield region was observed in different species or groups of closely related species (Harley, 1988; Prado & Gibbs, 1993; Taylor & Zappi, 2004). According to Prado (2000), migrations through Amazonia for species of tropical seasonal forests could have been promoted by the existence of a former dry vegetation belt connecting the Guayana Shield region with the Atlantic rain forest in Brazil (van der Hammen & Hooghiemstra, 2000). Finally, the basal position of *S. richii* within the clade *Corytholoma* and its endemism to the state of Veracruz in Mexico (Clayberg, 1968) imply a puzzling biogeographic scenario. Indeed, this geographic distribution and phylogenetic position indicate that a large geographic disjunction between the Brazilian Atlantic forest and Central America might have predated diversification in the clade *Corytholoma* (Fig. 4). This result suggests that *S. richii* could constitute a remnant of an early northward migration into Central America.

RELATIVE IMPORTANCE OF DISPERSAL AND VICARIANCE

Diversification in Sinningieae is associated with inter-area dispersal (20%), vicariance (23%), or within-area speciation (57%). The similarity between the frequency of dispersal and vicariance events can be explained by the alternating occurrence of these two processes during the diversification of the group. In southeastern Brazil, the majority of these reconstructed dispersal-vicariance episodes occurred between the coastal rain forest and adjacent inland areas characterized by a more seasonal climate (i.e., Paraná and São Francisco regions). These episodes initially consist of range expansions of rain forest lineages toward the interior followed by vicariance events that subsequently divide the source and the invaded areas. According to ancestral area optimization, these series of events occurred repeatedly at different heights in the phylogenetic tree and, therefore, probably occurred at different times. Cyclical range expansion-vicariance events may indicate the transitory nature of the barriers existing between coastal rain forest and neighboring inland areas. Climatic changes, especially in rainfall seasonality, may have been responsible for a succession of periods that either constrained or allowed expansion by producing more or less stringent ecological conditions toward the interior of Brazil. We hypothesize that this alternation between dispersal and vicariance along a changing climatic gradient has driven diversification of Sinningieae in the Brazilian Atlantic forests. Such a mechanism can be related to the species-pump hypothesis proposed by Stebbins (1974) in order to explain the high species richness of tropical forests bordered by tropical plant communities adapted to drier conditions.

In addition to inter-area biogeographic events, our results indicate that more than half of speciation events (57%) occurred within a single biogeographic area. For example, diversification of the *Sinningia* clade took place, in a large proportion, within the northern Atlantic rain forest (Fig. 2). To investigate the biogeographic circumstances of these speciation events, further biogeographic analyses at a finer scale are needed. A possible approach is to compare geographic distribution of sister taxa across all nodes in the phylogenetic tree (Barraclough & Vogler, 2000). Preliminary results in this direction indicate that, to a vast majority, diversification within a particular area might be the product of dispersal and allopatric isolation operating at a narrow geographic scale, in the context of the highly heterogeneous environment that characterizes the Brazilian Atlantic forests (Perret et al., unpublished data). We are convinced that such phylogenetic approaches at different geographic scales are necessary to assessing hypotheses about biological diversification in South America. Whether the results obtained for Sinningieae represent a general pattern of diversification can only be tested by evaluating their congruence with other plant or animal groups with high diversity in the Brazilian Atlantic forest hotspot.

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Appendix 1. Species analyzed in this study and vouchers of the specimens sequenced. Acronyms in parentheses indicate the herbarium where the vouchers are deposited.

Sinningieae: *Paliavana gracilis* (Mart.) Chautems, *Leoni 1812* (GFJP); *P. plumerioides* Chautems, *Chautems 460* (G); *P. prasinata* (Ker Gawl.) Benth., *Chautems & Perret 00-013* (G); *P. sericiflora* Benth., *Chautems 545* (G); *P. tenuiflora* Mansf., *Salviani 1541* (Instituto Plantarum); *P. werdermannii* Mansf., *Carvalho et al. 6552* (CEPEC); *Sinningia aggregata* (Ker Gawl.) Wiehler, *Chautems & Perret 97-001* (G); *S. aghensis* Chautems, *Pereira et al. 522* (VIES); *S. allagophylla* (Mart.) Wiehler, *Chautems 325* (G); *S. amambayensis* Chautems, *Salviani 1118* (Instituto Plantarum); *S. araneosa* Chautems, *Chautems & Perret 00-016* (G); *S. barbata* (Nees & Mart.) G. Nicholson, *Chautems & Perret 99-056* (G); *S. brasiliensis* (Regel & Schmidt) Wiehler & Chautems, *Chautems & Perret 97-002* (G); *S. bulbosa* (Ker Gawl.) Wiehler, *Chautems & Perret 97-003* (G); *S. calcaria* (Malme) Chautems, *Cervi et al. AC466* (UPCB); *S. canescens* (Mart.) Wiehler, *Chautems & Perret 97-004* (G); *S. carangolensis* Chautems, *Chautems 376* (G); *S. cardinalis* (Lehm.) H. E. Moore, *Chautems & Perret 97-015* (G); *S. cochlearis* (Hook.) Chautems, *Carvalho et al. AC535* (CEPEC); *S. concinna* (Hook. f.) Hanst., *Salviani 1540* (Instituto Plantarum); *S. conspicua* (Seem.) G. Nicholson, *Chautems & Perret 00-008* (G); *S. cooperi* (Paxton) Wiehler, *Chautems & Perret 01-032* (G); *S. curtiflora* (Malme) Chautems, *Cervi et al. AC477* (UPCB); *S. defoliata* (Malme) Chautems, *Chautems & Perret 01-031* (G); *S. douglasii* (Lindl.) Chautems, *Chautems & Perret 00-001* (G); *S. elatior* (Kunth) Chautems, *Salviani 1889* (Instituto Plantarum); *S. eumorpha* H. E. Moore, *Chautems & Perret 97-006* (G); *S. gigantifolia* Chautems, *Carvalho et al. AC529* (CEPEC); *S. glazioviana* (Fritsch) Chautems, *Chautems & Perret 97-017* (G); *S. guttata* Lindl., *Chautems & Perret 01-030* (G); *S. harleyi* Wiehler & Chautems, *Carvalho & Chautems 3235* (G); *S. hatschbachii* Chautems, *Chautems & Perret 99-065* (G); *S. hirsuta* (Lindl.) G. Nicholson, *Chautems & Perret 00-014* (G); *S. iarae* Chautems, *Carvalho et al. AC541* (CEPEC); *S. incarnata* (Aubl.) D. L. Denham, *Chautems & Perret 98-004* (G); *S. insularis* (Hoehne) Chautems, *Chautems & Perret 97-005* (G); *S. kautskyi* Chautems, *Chautems 390* (G); *S. lateritia* (Lindl.) Chautems, *Chautems & Barcia 321* (G); *S. leopoldii* (Planch.) Chautems, *Chautems & Perret 99-054* (G); *S. leucotricha* (Hoehne) H. E. Moore, *Chautems & Perret 97-008* (G); *S. lindleyi* Schauer, *Chautems & Perret 97-016* (G); *S. lineata* (Hjelmq.) Chautems, *Chautems & Perret 97-007* (G); *S. macrophylla* (Nees & Mart.) Benth. & Hook ex Fritsch, *Juchum et al. 001* (CEPEC); *S. macropoda* (Sprague) H. E. Moore, *Chautems & Perret 97-009* (G); *S. macrostachya* (Lindl.) Chautems, *Chautems & Perret 97-018* (G); *S. magnifica* (Otto & A. Dietr.) Wiehler, *Chautems & Perret 01-027* (G); *S. mauroana* Chautems, *Salviani 1542* (Instituto Plantarum); *S. micans* (Fritsch) Chautems, *Cervi et al. AC465* (UPCB); *S. nivalis* Chautems, *Chautems 354* (G); *S. nordestina* Chautems, Baracho & Siqueira Filho, *Baracho & Siqueira Filho 663/704* (G); *S. piresiana* (Hoehne) Chautems, *Salviani 840* (Instituto Plantarum); *S. pusilla* (Mart.) Baill., *Chautems & Perret 99-049* (G); *S. reitzii* (Hoehne) L. E. Skog, *Chautems & Perret 98-001* (G); *S. richii* Clayberg, *Chautems & Perret 01-029* (G); *S. rupicola* (Mart.) Wiehler, unknown; *S. sceptrum* (Mart.) Wiehler, *Carvalho et al. AC528* (CEPEC); *S. schiffneri* Fritsch, *Chautems & Perret 97-010* (G); *S. sellowii* (Mart.) Wiehler, *Chautems & Perret 01-028* (G); *S. speciosa* (Lodd.) Hiern, *Chautems & Perret 98-003* (G); *S. striata* (Fritsch) Chautems, *Chautems & Peixoto 366* (G); *S. tuberosa* (Mart.) H. E. Moore, *Chautems & Perret 00-009* (G); *S. tubiflora* (Hook.) Fritsch, *Chautems & Perret 97-011* (G); *S. valsuganensis* Chautems, *Chautems & Perret 99-061* (G); *S. villosa* Lindl., *Chautems & Perret 99-059* (G); *S. warmingii* (Hiern) Chautems, *Chautems & Perret 97-012* (G); *S.* sp. indet. 1, *Romero et al. 1709* (G); *S.* sp. indet. 4, *Chautems & Perret 99-051* (G); *S.* sp. indet. 7, *Cervi et al. AC484* (UPCB); *Vanhouttea brueggeri* Chautems, *Salimena Pires et al. AC501* (CESJ); *V. calcarata* Lem., *Carvalho et al. 526* (CEPEC); *V. fruticulosa* (Glaziou ex Hoehne) Chautems, *Chautems et al. 338* (G); *V. gardneri* (Hook.) Fritsch, *Chautems & Perret 01-024* (G); *V. hilariana* Chautems, *Salimena Pires et al. AC506* (CESJ); *V. lanata* Fritsch, *Carvalho et al. AC527* (CEPEC); *V. leonii* Chautems, *Leoni 4202* (GFJP); *V. pendula* Chautems, *Leoni 4197* (GFJP).

Gloxinieae: *Smithiantha laui* Wiehler, unknown.

Episcieae: *Nematanthus villosus* (Hanst.) Wiehler, *Chautems & Perret 99-041* (G).

Appendix 2. List of representative specimens for the 76 species of Sinningieae used to produce the maps on Figures 3 and 6. Specimens are organized alphabetically by species name. Acronyms in parentheses indicate the herbarium where the specimens are deposited.

Paliavana gracilis: BRAZIL. **Minas Gerais:** *Anderson 8875* (F, K, MO, NY, R, UB, US); *Irwin et al. 28622a* (NY); *Leoni 2849* (GFJP); *Leoni 4204* (GFJP).

Paliavana plumerioides: BRAZIL. **Minas Gerais:** *Arbo et al. 4384* (G, SPF); *Davis et al. 2285* (E, UEC).

Paliavana prasinata: BRAZIL. **Espírito Santo:** *Boone 668* (CEPEC, MBLM); *Boudet Fernandes et al. 2809* (MBLM); *Hatschbach & A. Cervi 51354* (CEPEC, MBM); *Hatschbach et al. 69163* (G, MBM); *Sazima 14056* (E, UEC). **Minas Gerais:** *Belém 1619* (CEPEC, UB); *Forzza et al. 2173* (G); *Leoni 290* (GFJP, US). **Rio de Janeiro:** *Braga & M. G. Bovini 3915* (RUSU); *Farney 736* (CEPEC, K, MG, NY); *Martinelli & M. Guerra 9847* (G, RB); *Mello Silva & J. R. Pirani 853* (NY, SPF); *Mello Silva et al. 2642* (G); *Pabst 8106* (HBR 31664); *Ribeiro & E. L. Costa 313* (RB); *Smith 6473* (IAN, NY, R, SP, US); *Strang 490* (GUA).

Paliavana sericiflora: BRAZIL. **Minas Gerais:** *Anderson 35809* (F, K, MO, NY, UB, US); *Anderson 8851* (F, K, MO, NY, US); *Arbo et al. 4566* (SPF); *Ferreira & B. V. Moreira 415* (G); *Gibbs et al. 5289* (MBM, SP, UEC).

Paliavana tenuiflora: BRAZIL. **Bahia:** *A. M. de Carvalho 7034* (CEPEC); *Alves 2005* (CEPEC); *Carvalho et al. 2384* (ALCB, CEPEC, K, MBM); *Esteves & R. P. Lyra-Lemos 2513* (SPF); *Giulietti et al. PCD 3309* (ALCB, CEPEC, SPF); *Harley 22320* (CEPEC, E, K, MO, US); *Mori et al. 10700* (CEPEC, US); *Santos 2717* (CEPEC, SEL, US). **Minas Gerais:** *Leoni 5570* (GFJP). **Paraíba:** *Felix 5688* (EAN). **Pernambuco:** *Andrade et al. 68* (G); *Felix & G. Dornelas 1120* (EAN 4211); *Felix & G. V. Dornelles 1316* (K); *Pietrobom-Silva et al. 4607* (MBM); *Siqueira Filho & J. A. Vicente 965* (G, UFP).

Paliavana werdermannii: BRAZIL. **Bahia:** *Harley et al. 54383* (HUEFS); *Roque et al. CFCR 14971* (ESA, G, SPF); *Roque et al. CFCR 15048* (SPF). **Minas Gerais:** *Cordeiro CFCR 834* (CEPEC, SPF, US); *Pirani et al. 2271* (NY, SPF); *Sakuragui et al. CFCR 15147* (BHCB, ESA, SPF).

Sinningia aggregata: BRAZIL. **Distrito Federal:** *Kirkbride 3703* (US). **Goiás:** *Irwin et al. 11808* (K, US); *Irwin et al. 34051* (F, NY, SEL, UB). **Mato Grosso:** *Ratter et al. 7586* (E). **Mato Grosso do Sul:** *Hatschbach et al. 35984* (F, M, MBM, MO, UEC, US, Z). **Minas Gerais:** *Alves 4378* (RB); *Castro 637* (G); *Chautems & M. Peixoto 461* (G); *Gouvea et al. 710* (UEC); *Melo & L. N. Asunção 1251* (BHCB); *Mota 172*

(G, BHCB 53328); *Shepherd et al. 3846* (MBM, NY, UEC). **Paraná:** *Cervi et al. 2047* (G); *Cervi et al. 3044* (G, NY, UPCB); *Dusén 15796* (G, K, MO isotype, S holotype); *Hatschbach 13900* (MBM); *Hatschbach 26350* (MBM, MO, US); *Hatschbach 3170* (HBR, MBM, PACA, UPCB); *Hatschbach 5061* (HBR, MBM, PACA, PKDC, UPCB); *Medri et al. 885* (UEC). **Rio de Janeiro:** *Andreata, R. et al. 542* (RB, RUSU); *Black & Fróes 11324* (IAN); *Flaster, B. 1196* (R); *Góes O. C. & Dionisio 456* (G, RB). **Santa Catarina:** *Hatschbach et al. 78061* (G); *Mattos 12036* (HAS, SP); *Reitz & R. M. Klein 4001* (HBR, NY, R, UC, US); *Reitz & R. M. Klein 5349* (B, F, NY, R, US); *Reitz 2031* (HBR, R, US); *Smith & R. M. Klein 14030* (B, BH, F, MO, NY, R, US, WIS). **São Paulo:** *Ferreira 3177* (GUA); *Mattos & Moura 14960* (SP); *Meira Neto 21332* (UEC, VIC); *Pires 676* (SP, SPF, cult. II.1952). PARAGUAY. **Amambay:** *Hassler, E. 11218* (G). **Cordillera:** *Zardini, E. & R. Degen 4009* (FCQ, G, US). **Paraguarí:** *Krapovickas, A. et al. 12265* (UC).

Sinningia aghensis: BRAZIL. **Espírito Santo:** *Boone 980* (CEPEC, MBML); *Shepherd et al. s.n.* (UEC 5893).

Sinningia allagophylla: ARGENTINA. **Chaco:** *Meyer, T. 17211* (LIL). **Corrientes:** *Ibarolla 3808* (LIL, MO). **Entre Rios:** *Burkart 24942* (SI). **Formosa:** *Morel 5314* (K, LIL). **Jujuy:** *Schulz, A. G. 8377* (NY). **Misiones:** *Montes, J. E. 471* (G, NY, US). BRAZIL. **Distrito Federal:** *Irwin et al. 26414* (F, K, MG, MO, NY, R, SEL, UB). **Goiás:** *Chautems 402* (G, UFG); *Hatschbach & J. M. Silva 59963* (G, UFP); *Hatschbach 42002* (MBM); *Melo & França 521* (SPF); *Rizzo 8845* (UFG). **Mato Grosso do Sul:** *Krapovickas & Cristóbal 34321* (MO). **Minas Gerais:** *Atkins et al. CFCR 13793* (SPF); *Cardoso 5691* (R); *Davidse et al. 10656A* (MO, SP); *Hatschbach 28650* (MBM); *Leoni 1436* (G, GFJP); *Macedo 2894* (MO, SP); *Mello Silva et al. 1624* (SP, SPF); *Williams & V. Assis 5565* (MO, US). **Paraná:** *Dusén 13456* (G, F, MO, NY, S, US); *Hatschbach 1899* (MBM, US); *Hatschbach 8577* (B, F, MBM, UPCB); *Krapovickas & Cristobal 39714* (MBM); *Kummrow & Graham 2644* (MBM, S, US); *Kummrow 966* (MU, NY). **Rio de Janeiro:** *Bello, W. 342* (R); *Mello Filho, L. E. & Dansereau 315* (R); *Martinelli, G. 8888* (CEPEC); *Vogel, S. 689* (US). **Rio Grande do Sul:** *Bueno 5423* (HAS); *Krapovickas & Cristobal 34176* (MBM); *Leite 668* (NY); *Mattos & N. Silveira 25343* (HAS); *Mattos 25429* (HAS); *Mattos et al. s.n.* (HAS); *Palacios-Cuezzo 1158* (MO); *Pivetta 817* (PACA); *Rambo 29391* (ICN); *Rossato et al. 5165* (NY, MO); *Senhem 4294* (B, HBR, INPA, MBM, PACA); *Silveira & D. Faria F°. 5423* (HAS); *Sobral & Esposito 3637* (F, MBM). **Santa Catarina:** *Chautems & R. Reitz 351* (G, HBR, US); *Klein 3339* (HBR); *Porto s.n.* (HAS); *Reitz & R. M. Klein 14019* (B, F, HBR, US, WIS); *Reitz 4910* (HBR, R, US); *Smith & R. M. Klein 10399* (GH, R, S, US); *Smith & R. M. Klein 11362* (B, NY, R, US); *Smith & R. M. Klein 14060* (US); *Smith & R. M. Klein 7438* (HBR, R, US); *Smith & R. Reitz 14276* (HBR, NY, US); *Smith & R. Reitz 8621* (HBR, R, US); *Smith et al. 9263* (HBR, NY, R, US); *Ule 1533* (P, PACA). **São Paulo:** *Buzato & M. Sazima 28017* (G, SPF); *Carvalho & J. R. Carvalho 11601* (UEC); *Cuatrecasas 26588* (US); *Eiten & L. T. Eiten 2432* (BH, NY, US); *Gemtchújnicov s.n.* (BOTU 12315); *Gibbs et al. 1707* (UEC); *Grotta s.n.* (SPF 15097); *Mimura 13* (NY, SP, US). PARAGUAY. **Alto Paraná:** *Schinini, A. 8107* (G). **Amambay:** *Schinini, A. & M. Dematteis 33459* (G). **Caaguazú:** *Schinini, A. 5772* (G). **Caazapá:** *Soria, N. 4032* (MO). **Canindeyú:** *Hassler, E. 4982* (G, GH, NY, P, S, UC, W). **Central:** *Schinini, A. 3734* (G). **Concepción:** *Fiebrig, K. 4626* (G, K). **Cordillera:** *Bordas, E. & G. Schmeda 4120* (FCQ, US). **Guairá:** *Jörgensen, P. 3729* (F, MO, NY, S). **Misiones:** *Schinini, A. & R. Vanni 26078* (G). **Paraguarí:** *Zardini, E. & T. Tilleria 30279* (G). **Presidente Hayes:** *Hassler, E. & T. Rojas 2657* (G, GH, NY, P, W). **San Pedro:** *Pedersen, T. M. 9451* (K, NY). URUGUAY. **Maldonado:** *Rosengurtt B 5242* (US). **Montevideo:** *Arechavaleta, J. 53* (G).

Sinningia amambayensis: PARAGUAY. **Amambay:** *Simonis, J. E., L. Pérez, W. J. Hahn & R. Duré Rodas 223* (G, MO, PY, RB, US).

Sinningia araneosa: BRAZIL. **São Paulo:** *Marcondes Ferreira et al. 783* (SP).

Sinningia barbata: BRAZIL. **Bahia:** *Carvalho et al. 7002* (CEPEC); *Hage 1541* (CEPEC, HUEFS); *Jardim et al. 990* (CEPEC); *Scardino & Grupo Pedra do Cavalo 408* (CEPEC, ALCB); *Silva 1486* (HUEFS); *Thomas et al. 11956* (CEPEC, NY); *Thomas et al. 9104* (CEPEC, NY). **Espírito Santo:** *Boone 219* (G, MBML); *Kollmann 2727* (MBML).

Sinningia brasiliensis: BRAZIL. **Bahia:** *França 1726* (HUEFS); *Carvalho & G. Lewis 911* (CEPEC, MBM); *Chautems et al. 226* (CEPEC); *França et al. 2304* (ESA); *Harley et al. 19418* (CEPEC, K); *Jardim et al. 1839* (CEPEC); *Santos 1645* (CEPEC, R). **Espírito Santo:** *Arbo et al. 5588* (K, SPF); *Kollmann et al. 2722* (G, MBML); *Sazima 14057* (UEC). **Minas Gerais:** *Belém 3770* (CEPEC, IAN, NY); *Giuletti et al. CFCR 6703* (CEPEC, G, K, SP, SPF); *Hatschbach 47816* (MBM, US); *Leoni 402* (GFJP); *Mota 1350* (G). **Rio de Janeiro:** *Sucre, D. & Braga 2655* (RB).

Sinningia bulbosa: BRAZIL. **Rio de Janeiro:** *Carauta, P 1686* (GUA, RB); *Farney, C. et al. 2438* (RB); *Martinelli, G. et al. 8520* (RB); *Smith, L. B. 6394* (R, UD); *Widgren R 870* (UPS).

Sinningia calcaria: BRAZIL. **Paraná:** *Hatschbach 32308* (BH, MBM, MO, WAG, Z); *Tiepolo & A. C. Svolenski 682* (MBM). **São Paulo:** *Fiaschi & A. C. Marcato 821* (G).

Sinningia canescens: BRAZIL. **Paraná:** *Chautems et al. 359* (FUEL, G, US); *Hatschbach & O. Guimarães 25477* (MBM, S, WAG); *Hatschbach 1036* (MBM, US); *Hatschbach 45657* (CEPEC, MBM). **São Paulo:** *Barreto et al. 3265* (SP).

Sinningia carangolensis: BRAZIL. **Minas Gerais:** *Leoni 586* (GFJP, R, US).

Sinningia cardinalis: BRAZIL. **Rio de Janeiro:** *Markgraf, F. 10084* (RB).

Sinningia cochlearis: BRAZIL. **Rio de Janeiro:** *Markgraf, F. 10471* (RB).

Sinningia conspicua: BRAZIL. **Paraná:** *Dusén 16543* (S). **Santa Catarina:** *Smith & R. M. Klein 14168* (R, US).

Sinningia cooperi: BRAZIL. **Espírito Santo:** *Kollmann & E. Bausen 5670* (MBML). **Minas Gerais:** *Leoni 4950* (GFJP). **Paraná:** *Hatschbach 12400* (MBM, WAG); *Hatschbach 18578* (F, MBM); *Santos et al. 763* (G). **Rio de Janeiro:** *Martinelli, G. & Maas, P. 3276* (RB). **Santa Catarina:** *Dusén s.n.* (F, GH, S); *Reitz & R. M. Klein 6551* (HBR, NY, UC, US). **São Paulo:** *Buzato & M. Sazima 26868* (G, UEC).

Sinningia curtiflora: BRAZIL. **Paraná:** *Chautems & A. Cervi 332* (G, UPCB, US); *Gentry & E. Zardini 49756* (MBM, RBR, US). **Rio Grande do Sul:** *Silveira 10619* (HAS). **Santa Catarina:** *Reitz & R. M. Klein 4105* (G, NY, UC, US); *Reitz & R. M. Klein 8270* (G, NY, UC, US); *Reitz C1427* (GH, HBR, R). **São Paulo:** *Miyagi et al. 439* (ESA, HRCB, SP, SPF).

Sinningia defoliata: BRAZIL. **Goiás:** *Irwin & Soderstrom 7371* (BH). **Mato Grosso:** *Dorrien Smith 308* (K). **Minas Gerais:** *Macedo 3882* (SP, US).

Sinningia douglasii: ARGENTINA. **Misiones:** *Renvoize, S. A. 3245* (K). BRAZIL. **Minas Gerais:** *Leoni 3495* (GFJP); *Meireles & M. M. F. A. Pereira 660* (UEC); *Tamashiro et al. 1283* (UEC). **Paraná:** *Chagas e Silva & Soares 908* (FUEL, MBM); *Dusén 7045* (MO, S); *Hatschbach 1080* (LIL, MBM, US); *Hatschbach 22364* (MBM); *Hatschbach 32866* (MBM);

Hatschbach 3390 (MBM); *Hatschbach 40179* (MBM, NY, UEC); *Koczicki 267* (MBM); *Lindeman & J. H. Haas 3149* (NY). **Rio de Janeiro:** *Carvalho, A. M. & Martinelli, G. 1* (CEPEC, G, RB); *Martinelli, G. et al. 17779* (RB); *Pessoa, S. V. A. 109* (RB). **Rio Grande do Sul:** *Camargo 2606* (B, PACA); *Friderichs s.n. PACA 30678* (B, PACA); *Silveira 5889* (HAS); *Silveira 7304* (HAS); *Waechter 1793* (HAS, ICN). **Santa Catarina:** *Klein & A. Bresolin 7670* (HBR); *Klein 1755* (HBR, US); *Mattos 22742* (HAS); *Reitz & R. M. Klein 12518* (HBR, NY, R, US); *Reitz & R. M. Klein 13532* (HBR); *Reitz & R. M. Klein 7345* (HBR); *Reitz & R. M. Klein 7553* (HBR); *Reitz & R. M. Klein 9286* (HBR); *Reitz 5909* (HBR); *Reitz C762* (HBR, RB); *Smith & R. M. Klein 13363* (US); *Smith & R. M. Klein 7338* (HBR, S, US); *Smith & R. Reitz 8853* (HBR, US). **São Paulo:** *Barros & J. E. L. S. Ribeiro 2034* (SP); *Carmello et al. 77* (BOTU, G); *Gibbs et al. 3251* (MBM, NY, UEC); *Leitão Filho 32912* (UEC); *Leitão Filho et al. 3167* (MBM, NY, UEC); *Romaniuc Neto & A. Custodio Filho 247* (SP); *Shirasuna et al. 51* (SP).

Sinningia elatior: ARGENTINA. **Corrientes:** *Krapovickas, A. et al. 29369* (G, MBM, MO). **Entre Ríos:** *Burkart, A. & S. Crespo s.n.* (Her. Burkart, SI). **Misiones:** *Rodríguez 718* (BAFC, LIL, SI, US). BOLIVIA. **Beni:** *Beck, S. G. 13143* (G). **La Paz:** *Solomon, J. C. 9339* (MO, NY, US). **Santa Cruz:** *Steinbach, R. F. 814* (F, G, MO, NY, US). **Yungas:** *Bang, M. 543* (F, MO, NY, US). BRAZIL. **Amazonas:** *Harley et al. 19757* (CEPEC, G, K); *Janssen 209* (INPA, M, MG, SP); *Traill 521* (K). **Bahia:** *França 1267* (HUEFS); *Harley et al. 19757* (CEPEC, K); *Harley et al. 22323* (CEPEC, K). **Distrito Federal:** *Irwin et al. 8951* (F, K, NY, UB, US). **Espírito Santo:** *Folli 2403* (RB). **Goiás:** *Anderson 6276* (NY); *Ferreira et al. 2658* (UFG); *Hunt & Ramos 5725* (SP); *Irwin et al. 13506* (UB); *Irwin et al. 18839* (F, NY, UB, W); *Irwin et al. 24168* (BH, F, IAN, K, NY, US); *Irwin et al. 25394* (F, NY, UB); *Maguire et al. 56981* (NY, UB); *Rizzo & A. Barbosa 3354* (UFG); *Thomas et al. 5786* (SPF). **Mato Grosso:** *Ekman da Silva et al. R 7110* (R 7110); *Hatschbach 33275* (Z); *Hatschbach 34143* (MBM); *Hoehne 569/Rondon 3684* (R); *Hunt & J. F. Ramos 5725* (K, NY, UC, UB); *Philcox & A. Ferreira 3684* (K); *Philcox & J. F. Ramos 4393* (K, NY, UB); *Pires & M. R. Santos 16587* (MG); *Saddi et al./UFMT 213* (UFMT). **Mato Grosso do Sul:** *Armando & Gerra s.n.* (G, RB 102323); *Garcia s.n.* (UEC 13928); *Hunt & J. F. Ramos 5959* (K); *Rodrigues et al. 322* (RB); *Sucre 10554* (RB); *Tsugaru & H. A. Guinoza B-2085* (MO, NY). **Minas Gerais:** *Assis & M. K. Ladeira 621* (G); *Brade & Altamiro 50* (R); *Cavalcanti et al. CFSC 9408* (SPF); *Cordeiro & Simonis CFCR 1021* (SPF, US); *Irwin et al. 20880* (F, MO, NY, RB, UB); *Irwin et al. 23774* (BH, F, IAN, K, NY, UB, US); *Irwin et al. 26052* (F, IAN, NY, RB, UB, W); *Krieger 20588* (CESJ); *Macedo 2213* (MO, US); *Pirani et al. 3867* (G, SPF); *Romero et al. 1696* (G); *Romero et al. 5147* (UEC); *Sakuragui et al. CFCR 15087* (SPF); *Salimena Pires et al. AC-492* (CESJ, G); *Shepherd 493* (UEC); *Warming s.n.* (US). **Pará:** *Pires et al. 6120* (IAN, NY). **Paraná:** *Hatschbach 18227* (MBM, UPCB); *Hatschbach 22884* (MBM, NY); *Hatschbach 24125* (MBM, MO, UPCB); *Hatschbach 26221* (M, MBM, MO); *Hatschbach 26411* (MBM, Z); *Hatschbach 5466* (MBM); *Hatschbach 580* (MBM, PACA); *Hatschbach 615* (MBM, PACA, SP); *Kummrov & J. D. Stutts 1791* (MBM); *Reitz & Klein 17637* (F, US); *Santos et al. 650* (G); *Yunigoshi & R. Kummrov 4597* (CEPEC, MBM, US). **Rio Grande do Sul:** *Bueno 4751* (HAS); *Jürgens 193* (B); *Mattos & Mattos 23178* (HAS); *Mattos et al. 22012* (HAS); *Rambo & Schultz 36505* (ICN); *Rambo [37449/34749?]* (MO); *Rambo 10083* (PACA); *Rambo 28483* (PACA); *Rambo 34749* (PACA, S); *Rambo 38674* (PACA); *Rambo 56662* (B, HBR, PACA); *Rambo 63645* (B, S); *Rambo 9892* (PACA); *Silveira 3847* (HAS); *Silveira 6047* (HAS); *Waechter 1977* (ICN). **Santa Catarina:** *Reitz & R. M. Klein 14403* (R); *Reitz 4618* (HBR, UC, US); *Reitz C1406* (GH, HBR, NY, UC, US); *Senhem 5456* (HBR); *Smith & R. M. Klein 10577* (HBR, NY, R, RB, UC, US); *Smith & R. Reitz 8619* (HBR, R, US). **São Paulo:** *Amaral Jr. 1209* (BOTU, G); *Custodio Filho 2150* (SP, SPSF); *Hatschbach & Kummrow 37122* (COI, MBM, MU); *Lutz & B. Lutz 1931* (R); *Mimura 271* (SP, US); *Muller 32172* (UEC); *Ratter et al. 4980* (NY, UEC); *Souza et al. 7250* (HRCB, SP, SPF, UEC); *Sugiyama & Mantovani 128* (SP). **Tocantins:** *Gardner 3872* (K). COLOMBIA. **Casanare:** *Uribe Uribe, L. 3758* (NY). **Guaviare:** *Cardenas, D. et al. 6490* (COAH, MO). **Meta:** *García, M. C. et al. 524* (US). PARAGUAY. **Amambay:** *Solomon, J. C. et al. 7128* (MO, PY). **Caaguazú:** *Krapovickas, A. et al. 12559* (UC). **Caazapá:** *Basualdo, I. 2709* (MO). **Canindeyú:** *Schinini, A. & M. Dematteis 33317* (G). **Central:** *Pedersen, T. M. 9496* (K). **Concepción:** *Pedersen, T. M. 3103* (P). **Cordillera:** *Zardini, E. 8176* (US). **Guairá:** *Schinini, A. 2091* (G). **Misiones:** *Pedersen, T. M. 1406* (US). **Paraguarí:** *Zardini, E. 8685* (US). **San Pedro:** *Hassler, E. 4501* (G, GH, K, NY, P, UC, W). PERU. **Amazonas:** *Díaz, C. & Campos, J. 3637* (MO). **Cajamarca:** *Weberbauer, A. 6152* (F, US). **Cuzco:** *Vargas Calderón, J. C. 17278* (US). **Junín:** *Smith, D. N. 6534* (MO). **Madre de Dios:** *Gentry, A. & Núñez, P. 69460* (MO). **San Martín:** *Woytkowski, F. 6231* (MO). URUGUAY. **Montevideo:** *Rosengurtt B 2574* (F). VENEZUELA. **Amazonas:** *Gentry, A. & Berry, P. 14655* (MO, VEN). **Apure:** *Davidse, G. & González, A. 15739* (MO). **Aragua:** *Williams, L. 10146* (F, VEN). **Bolívar:** *Steyermark et al. 131788* (MO, VEN). **Carabobo:** *Pittier 9037* (NY, US); *Rávago, C. 301* (VEN). **Guárico:** *Aristeguieta, L. 6190* (NY, US, VEN). **Miranda:** *Pittier 7508* (US). **Monagas:** *Maguire, B. et al. 35828* (NY); *Wurdack, J. & Monachino, J. 39537* (NY).

Sinningia eumorpha: BRAZIL. **São Paulo:** *Costa s.n.* (R 203451); *SanMartin-Gajardo s.n.* (UEC 35824).

Sinningia gigantifolia: BRAZIL. **Minas Gerais:** *Guillaumon s.n.* (SPFS); *Leoni 4569* (GFJP); *Yamamoto* (UEC). **Rio de Janeiro:** *Martinelli, G. et al. 13409* (RB); *Martinelli, G. & Farney, C. 8688* (RB); *Silva Neto, S. J. et al. 1185* (RB); *Snow, D. 20* (K); *Sucre, D. & Braga 2318* (R, RB). **São Paulo:** *Arzolla & G. C. R. de Paula 411* (SPSF).

Sinningia glazioviana: BRAZIL. **São Paulo:** *Freitas 256* (G); *Shirasuna et al. 75* (SP, UEC).

Sinningia guttata: BRAZIL. **Rio de Janeiro:** *Kuhlmann 6056* (RB).

Sinningia harleyi: BRAZIL. **Bahia:** *Carvalho & A. Chautems 3235* (CEPEC, holotype); *Harley et al. 51552* (HUEFS).

Sinningia hatschbachii: BRAZIL. **Paraná:** *Hatschbach 23939* (MBM, NY, UC, WAG). **São Paulo:** *Chautems s.n. AC-1479* (G).

Sinningia hirsuta: BRAZIL. **Rio de Janeiro:** *Farney, C. & J. C. Gomes 4157* (RB); *Vidal II-5544* (R).

Sinningia iarae: BRAZIL. **São Paulo:** *Mendonça 13* (R); *Silveira 9861* (HAS).

Sinningia incarnata: BRAZIL. **Amapá:** *Fróes, R. L. 25820* (IAC, IAN, UB); *Pires, J. M. & P. C. Cavalcante 52651* (NY). **Amazonas:** *Ducke, A. s.n.* (G, RB 37615); *Nascimento, O. C. et al. 144* (RB); *Poole, J. M. 1817* (MG). **Ceará:** *Lima Verde 13* (G). **Maranhão:** *Eiten, G. & Eiten 4343* (MO, NY, SP, US). **Pará:** *Ducke, A. 810* (RB). **Pernambuco:** *Pickel 3060* (F, IPA, S, US). **Roraima:** *Black & Magalhães 51-12888* (IAN, UB); *Ducke, A. s.n.* (CEPEC, G, RB); *Milliken, W. & Bowles 397* (E, G, K, NY); *Sette Silva, E. L. 503* (NY). **Tocantins:** *Plowman et al. 8156* (INPA, MG, NY, SEL, US).

COLOMBIA. **Cauca:** *Cuatrecassas, J. 19538* (F, MO, NY, US). **Cundinamarca:** *Pennell, F. W. 2733* (F, MO, NY, US). **Magdalena:** *Seifriz, W. 553* (US). **Meta:** *Grant, M. L. 9220* (NY, US). **Tolima:** *Uribe Uribe, L. 1690* (US). COSTA RICA. **Anajuela:** *Utley, J. & Utley, K. 2626* (MO). **Guanacaste:** *Webster, G. & Raveret, M. 22177* (F). EL SALVADOR. **Ahuachapán:** *Croat, T. 42107* (MO). **La Libertad:** *Dwyers, J. D. 427* (MO). **Sonsonate:** *Croat, T. 42259* (MO). FRENCH GUIANA. **Bassin de l'Oyapock:** *Prevost, M. F. & P. Grenand 2050* (CAY, K). **Bassin du Ha:** *Granville, J. et al. 9780* (P). GUATEMALA. **Baja Veracruz:** *Harmon, W. E. & J. D. Dwyer 3048* (MO). **Chiquimula:** *Molina, A. & Molina 26774* (F); *Standley, P. C. 74467* (F). **Huehuetenan Goiás:** *Steyermark, J. 50795* (F). **Jutiapa:** *Steyermark, J. 30366* (F). **Quiché:** *Aguilar, J. I. 1433* (F). **Santa Rosa:** *Harmon, W. E. & J. D. Dwyer 3233* (MO). **Zacapa:** *Steyermark, J. 29533* (F). GUYANA. **Upper Takutu–Upper Essequibo:** *Gillespie, L. J. 1993* (CAY). HONDURAS. **Comayagua:** *Webster, G. et al. 12727* (F, MO). **Copán:** *Croat, T. 42514* (MO). **El Paraíso:** *Molina R. A. 14614* (F, NY). **Morazán:** *Williams, L. O. & Molina A. R. 13289* (F). **Ocotepeque:** *Molina R. A. & Molina 31080* (F, MO). **Santa Bárbara:** *Molina R. A. 21974* (F). **Valle:** *Molina R. A. & Molina 22791* (F, NY). MEXICO. **Chiapas:** *Breedlove, D. E. 27103* (MO, NY). **Oaxaca:** *King, M. R. 1958* (NY). **Veracruz:** *Moore, H. E. 8058* (BH). NICARAGUA. **Chontales:** *Stevens, W. D. et al. 20552* (MO). **Esteli:** *Stevens, W. D. & Krukoff 2986* (MO). **Madriz:** *Moreno, P. P. 17710* (MO). **Masaya:** *Stevens, W. D. 4237* (MO). **Matagalpa:** *Moreno, P. P. 17710* (MO). **Nueva Segovia:** *Stevens, W. D. & Krukoff 3302* (MO). **Rio San Juan:** *Seymour, F. C. & Robbins, S. B. 6191* (MO). PANAMÁ. **Canal Area:** *Dressler, R. L. 5037* (F, MO). **Coclé:** *Luteyn, J. L. 1244* (F, MO). **Panama:** *Hammel, B. 3755* (MO). SURINAM. **Sipaliwini:** *Granville, J. et al. 13738* (CAY, US); *Oldenburger, F. 866* (NY). VENEZUELA. **Amazonas:** *Davidse, G. & Miller G. 27300* (VEN). **Aragua:** *Bunting, G. S. 4518* (F, K). **Bolívar:** *Steyermark, J. 131258* (MO). **Distrito Federal:** *Steyermark, J. 97253* (US). **Mérida:** *Steyermark, J. 56358* (F, US). **Miranda:** *Aristeguieta, L. 3206* (NY). **Tachira:** *Werff, H. van der & González, A. 5360* (MO).

Sinningia insularis: BRAZIL. **São Paulo:** *Rossi et al. 435* (SP).

Sinningia kautskyi: BRAZIL. **Espírito Santo:** *Chautems & M. Peixoto 269* (Herbarium UFES, Vitória, holotype).

Sinningia lateritia: BRAZIL. **Rio de Janeiro:** *Chautems, A. & Barcia 321* (G, R); *Martinelli, G. et al. 10688* (RB).

Sinningia leopoldii: BRAZIL. **Santa Catarina:** *Cervi et al. AC-483* (G, UPCB); *Reitz 4549* (HBR, US).

Sinningia leucotricha: BRAZIL. **Paraná:** *Motosima s.n.* (SP 56347). **Santa Catarina:** *Reitz & R. M. Klein 13603* (HBR).

Sinningia lindleyi: BRAZIL. **Rio de Janeiro:** *Araujio & Vianna 926* (GUA).

Sinningia lineata: BRAZIL. **Rio Grande do Sul:** *Hatschbach et al. 78338* (G); *Silveira & C. J. Manson 6071* (HAS). **Santa Catarina:** *Chautems & R. Reitz 348* (G, HBR, US).

Sinningia macrophylla: BRAZIL. **Bahia:** *Thomas et al. 11936* (CEPEC, NY).

Sinningia macropoda: BRAZIL. **Paraná:** *Carneiro 317* (MBM); *Chautems et al. 360* (FUEL, G); *Hatschbach 1035* (MBM, US); *Hatschbach 45655* (CEPEC, MBM, MO, Z); *Vieira et al. 131* (FUEL). **São Paulo:** *SanMartin-Gajardo s.n.* (UEC 35826). PARAGUAY. **Paraguarí:** *Hahn, W. J. 2687* (G, PY, US).

Sinningia macrostachya: BRAZIL. **Rio Grande do Sul:** *Bueno 1947* (F, HAS, US); *Chautems & J. Waechter 330* (G, ICN, US); *Costa Sacco 1226* (F, HAS, HBR, IAN, R); *Meyer et al. 63* (HAS); *Rambo 51594* (B, S, US); *Senhem 3630* (B, MBM); *Silveira 173* (HAS); *Silveira 6869* (HAS); *Sobral & C. Grabanska 3936* (ICN); *Sobral et al. 4232* (ICN); *Stehmann et al. 1308* (UEC). **Santa Catarina:** *Hatschbach et al. 61239* (G); *Reitz & R. M. Klein 9241* (HBR, R).

Sinningia magnifica: BRAZIL. **Espírito Santo:** *Hatschbach 47696* (CEPEC, MBM, SPF, US); *Kollmann & C. Fraga 3210* (MBML). **Minas Gerais:** *Chautems & M. Peixoto 364* (G); *Cosenza 23462* (CESJ); *Dulith 31207* (UEC); *Furlan et al. CFCR 3061* (CEPEC, SPF, US); *Grandi 1651* (FCAB, G); *Irwin et al. 29051a* (F, K, MO, NY, US); *Mayo et al. CFSC 7092* (CEPEC, G, SPF, US); *Oliveira & F. R. Salimena CESJ 24790* (CESJ); *Stehmann et al. 2454* (G). **Rio de Janeiro:** *Forzza et al. 3419* (G); *Gotsberger & G. Gottsberger 117-16471* (G); *Pereira 1286* (R). **São Paulo:** *Handro s.n. SP 39421* (SP 39421); *Tamashiro et al. 847* (HRCB, SP, UEC).

Sinningia mauroana: BRAZIL. **Paraná:** *Hatschbach 14149* (MBM, NY, S). **São Paulo:** *Barros 2250* (G, NY, SP); *Chautems & M. Peixoto 283* (CEPEC holotype; G, US, isotypes); *Kirizawa 2787* (SP); *Silveira 9862* (HAS).

Sinningia micans: BRAZIL. **São Paulo:** *Dedecca Kug & Gardini s.n. IAC 8338* (IAC 8338); *Wettstein & Schiffner s.n.* (WU sintipo *Corytholoma micans* Fritsch).

Sinningia nivalis: BRAZIL. **Rio Grande do Sul:** *Bueno 3062* (HAS); *Rambo 56197* (B, HBR). **Santa Catarina:** *Hatschbach et al. 78119* (G); *Pereira s.n.* (HBR, NY, R, US).

Sinningia nordestina: BRAZIL. **Alagoas:** *Cervi et al. 6017* (G). **Bahia:** *Santos 5* (ALCB). **Ceará:** *Eugenio Leite 1073* (RB). **Paraíba:** *Agra et al. 1461* (G, JPB). **Pernambuco:** *Andrade-Lima 20* (IPA); *Pietrobom-Silva et al. 4602* (MBM, SPF, UFP); *Siqueira Filho & G. Baracho 663/704* (G isotype, UFP holotype). **Sergipe:** *Viana 1026* (ASE); *Viana 652* (ASE).

Sinningia piresiana: BRAZIL. **São Paulo:** *Macedo 275* (ESA); *Pires s.n.* (SP 56345 holótipo de *Rechsteineria piresiana*, *Salino 130*, ESA).

Sinningia pusilla: BRAZIL. **Rio de Janeiro:** *Braga, J. M. 715* (RUSU); *Mello Filho, L. E. & Emmerich, M. 3121* (R).

Sinningia reitzii: BRAZIL. **Santa Catarina:** *Reitz & R. M. Klein 4068* (B, G, HBR holotype, MBM, NY, PACA, R, SP, UC); *Silveira 9716* (HAS).

Sinningia richii: MEXICO. **Veracruz:** *Clayberg 26* (BH).

Sinningia rupicola: BRAZIL. **Minas Gerais:** *Braga et al. s.n.* (G); *Irwin et al. 19805* (F, K, MO, NY, UB, US); *Stehmann & C. E. S. Ferreira 2404* (G).

Sinningia sceptrum: BRAZIL. **Bahia:** *Lewis 737* (CEPEC, K). **Espírito Santo:** *Arbo et al. 7720* (CEPEC); *Kollmann 64* (MBML, UEC); *Sucre 5585* (CEPEC, RB). **Minas Gerais:** *Assis et al. 959* (G); *Leoni 1513* (GFJP); *Leoni 3243* (GFJP); *Mexia 4343* (F, MO, NY, S, VIC, US); *Moreira & S. H. Borges 24583* (CESJ). **Rio de Janeiro:** *Duarte, A. 6298A* (G, RB); *Laclette, P. 921* (R); *Yamamoto, K. & Viera, A. O. S. 26212* (UEC).

Sinningia schiffneri: BRAZIL. **Rio de Janeiro:** *Silveira, N. 9855* (HAS). **São Paulo:** *Cordeiro 2377* (NY, SP); *Cordeiro et al. 525* (G); *Gomes da Silva et al. 277* (RB, SPF); *Leitão Filho et al. 34616* (SP); *Wettstein & Schiffner s.n.* (WU holotype).

Sinningia sellovii: ARGENTINA. **Corrientes:** *Utter & Lonsdale 60-341* (K). **Misiones:** *Eskuche 1999* (Z). BOLIVIA. **Chuquisaca:** *Beck, S. G. 9356* (G). **Santa Cruz:** *Mello Silva, R. et al. 2079* (RB). BRAZIL. **Mato Grosso do Sul:** *Hatschbach et al. 74337* (G). **Paraná:** *Dusén 8944* (S); *Hatschbach 22899* (MBM, UPCB); *Hatschbach 23136* (F, NY,

MO); *Hatschbach 31052* (MBM, US, Z); *Lindeman & J. H. Haas 3271* (K, NY, US); *Poliquesi & J. Cordeiro 268* (G). **Rio Grande do Sul:** *Albuquerque s.n.* (HAS); *Bueno 3266* (HAS); *Bueno 5187* (HAS); *Chautems & J. Waechter 373* (G); *Eggli et al. 2488* (ZSS); *Lindman A1297* (S, UPS); *Mattos & N. H. Bassan 28573* (HAS); *Mattos & N. Mattos 24680* (HAS); *Mattos & N. Mattos 31062* (HAS); *Mattos & N. Silveira 23305* (ICN); *Mattos & N. Silveira 26437a* (ICN); *Mattos & N. Silveira 26968* (HAS); *Mattos & R. Frosi 23743* (HAS); *Meyer et al. 65* (HAS); *Senhem 3631* (ALCB, B, INPA, MBM); *Silveira & J. Mansan 6065* (HAS); *Waechter 1840* (ICN). **Santa Catarina:** *Chautems & R. Reitz 347* (G, HBR, US); *Reitz 3785* (HBR, US); *Smith & R. M. Klein 13838* (NY, R, US). PARAGUAY. **Amambay:** *Brunner, D. R. et al. 956* (PY). **Canindeyú:** *Fernández Casas, J. & J. Molero 4195* (G). **Concepción:** *Anisits, J. D. 2704* (S). **Guairá:** *Basualdo, I. 1800* (MO). **Paraguarí:** *Bernardi, L. 18146* (F, G, MO, NY). URUGUAY. **Rivera:** *Herter W. G. 1387* (F, MO, Z).

Sinningia speciosa: BRAZIL. **Bahia:** *Mori 10714* (CEPEC, NY). **Espírito Santo:** *Boone 967* (CEPEC, MBML); *Martinelli et al. 2206* (US); *Mattos & Bicalho 10857* (HAS, SP). **Minas Gerais:** *Leoni s.n.* (CEPEC, GFJP 398). **Rio de Janeiro:** *Araujo, D. & Souza, S. R. 8222* (GUA); *Braga* (photo); *Mello Filho, L. E. 2611* (R); *Segadas-Viana, F. 4469* (R); *Sucre, D. 9731* (BH, CEPEC).

Sinningia striata: BRAZIL. **Minas Gerais:** *Krapovickas & Cristobal 35450* (MO, NY, US).

Sinningia tuberosa: BRAZIL. **Minas Gerais:** *Andrade & Renato 927* (BHCB 15843); *Irwin et al. 29414* (F, K, NY, UB, US); *Mello Silva et al. 1653* (RB, SP, SPF). **Rio de Janeiro:** *Duarte, A. 4278* (RB).

Sinningia tubiflora: ARGENTINA. **Chaco:** *Schulz 850* (K, LIL). **Córdoba:** *Stuckert, T. 19596* (G). **Corrientes:** *Schwarz 8818* (NY, LIL). **Entre Rios:** *Burkart 24023* (SI). **Formosa:** *Morel 1743* (LIL). **Santa Fé:** *Maldonado, R. 1731* (K). **Santiago del Estero:** *Maldonado 975* (LP); *Maldonado Bruzone 1568* (LP). PARAGUAY. **Central:** *Hassler, E. 1476* (G, K, NY, P). **Concepción:** *Krapovickas, A. & C. L. Cristóbal 45088* (G). **Neembucu:** *Meyer, T. 15939* (LIL). **Presidente Hayes:** *Brunner, D. R. 1334* (PY, US). **San Pedro:** *Hassler, E. 6023* (G, NY, S, UC).

Sinningia valsuganensis: BRAZIL. **Espírito Santo:** *Boone 1104* (CEPEC, MBML, MO); *Rossini, A. Chautems & M. Peixoto 555* (MBML).

Sinningia villosa: BRAZIL. **Bahia:** *Jardim 3945* (NY, HUEFS). **Espírito Santo:** *Kollmann et al. 1683* (G, MBML). **Minas Gerais:** *Andrade & M. A. Lopes 676* (CEPEC, G).

Sinningia warmingii: ARGENTINA. **Catamarca:** *Castillon 1717* (LIL, US). **Chaco:** *Aguilar, R. M. 973* (G, LIL, US 2123801). **Corrientes:** *Pedersen, T. M. 10861* (NY, MO). **Formosa:** *Morel, I. 2065* (G, LIL). **Jujuy:** *Mello Silva, R. et al. 1900* (G). **Salta:** *Novara, L. J. s.n.* (MO 3099831). **Tucumán:** *Olar, D. 53* (NY). BOLIVIA. **Santa Cruz:** *Herzog 1170* (G, S, L, W, Z). **Tarija:** *Fiebrig 2109* (B not extant). BRAZIL. **Minas Gerais:** *Anderson et al. 36287* (F, K, MO, NY, UB, US); *Melo & J. A. Lombardi 396* (G). **Paraná:** *Hatschbach 22893* (F, HBR, K, MBM, MO, NY). **Rio de Janeiro:** *Araujio, D. & Maciel, N. C. 8655* (GUA). **Rio Grande do Sul:** *Bueno 2007* (HAS); *Hatschbach 31177* (MBM, Z); *Mattos et al. 29147* (HAS); *Meyer et al. 198* (HAS); *Rambo 52123* (HBR, PACA, S); *Silveira 6569* (HAS); *Silveira et al. 1156* (HAS). **Santa Catarina:** *Hatschbach et al. 79222* (G); *Lourteig 2120* (HBR, P, S, US); *Lourteig 2324* (HBR, US); *Reitz & R. M. Klein 7990* (G, HBR, NY, UC, US); *Reitz C411* (HBR, R, RB); *Ule 1058* (US). **São Paulo:** *Edwall s.n. CGG 5906* (SP). ECUADOR. **Loja:** *Harling, G. & Anderson, L. 22594* (GB, MO, US). PARAGUAY. **Alto Paraguay:** *Mereles, F. & L. Ramella 2886* (G). **Amambay:** *Hassler, E. 8491* (G, NY). **Central:** *Zardini, E. 23602* (MO). **Concepción:** *Fiebrig, K. 4668* (G, GH, HBG, M). **Cordillera:** *Fiebrig, K. 825* (K, E, F, G, HBG, P). **Ñeembucú:** *Bernardi, L. 20474* (G). **Presidente Hayes:** *Zardini, E. et al. 2625* (US). **San Pedro:** *Hassler, E. 6022* (G, GH, NY, P, S, UC, W). PERU. **Amazonas:** *Wolfe, F. H. & F. H. Dobson 816* (CONN). **Apurimac:** *Alfaro, R. C. 3364* (MO). **Cajamarca,** *Sánchez Vega, I. M. et al. 5831* (F, MO, NY, US). **Cuzco:** *Croat, T. 50964* (MO); *Diehl, A. 2512* (F). **Huancavelica:** *Weberbauer, A. 6446* (F). **Junin:** *Ochoa, C 204* (US). **La Libertad:** *Vásques, N. 6310* (US). **Lambayeque:** *Llatas Quiroz, S. & Cruz, H. 1191* (GB). **Lima:** *Soukup, J. 4186* (US). **Puno:** *Vargas C. 14826* (US).

Sinningia sp. indet. 1: BRAZIL. **Minas Gerais:** *Nakajima & André 2481* (UEC); *Simão Bianchini & S. Bianchini 1202* (SP).

Sinningia sp. indet. 4: BRAZIL. **Paraná:** *Hatschbach 33846* (MBM, Z). **São Paulo:** *Barbosa et al. 884* (G).

Sinningia sp. indet. 7: BRAZIL. **Rio Grande do Sul:** *Silveira 8824* (G, HAS); *Waechter 2282* (ICN). **Santa Catarina:** *Hatschbach et al. 27241* (MBM holotype, BH isotype, NY, UC).

Vanhouttea brueggeri: BRAZIL. **Minas Gerais:** *Brugger & H. G. Souza s.n.* (CESJ 24699a); *Forzza et al. 1803* (G).

Vanhouttea calcarata: BRAZIL. **Espírito Santo:** *Brade 19829* (R, RB); *Kollmann et al. 2336* (G, MBM, MBML). **Minas Gerais:** *Hatschbach 47674* (MBM, US); *Krieger & Roth 1044* (R, SP). **Rio de Janeiro:** *Anderson 11719* (NY, US); *Boudet Fernandes 784* (GUA); *Costa et al. 493* (CEPEC, G, RB, SP); *Martinelli & C. Farney 8690* (RB, US).

Vanhouttea fruticulosa: BRAZIL. **Rio de Janeiro:** *Chautems et al. 338* (G, RB, US).

Vanhouttea gardneri: BRAZIL. **Rio de Janeiro:** *Anderson 11722* (NY, US); *Oliveira 598* (GUA); *Smith 6687* (NY, R, SP, US).

Vanhouttea hilariana: BRAZIL. **Minas Gerais:** *Andrade 921* (CESJ, RB); *Farney & S. A. Geromel 1065* (G); *Lombardi et al. 4679* (G).

Vanhouttea lanata: BRAZIL. **Rio de Janeiro:** *Mello Silva et al. 2619* (G); *Ribeiro et al. 788* (GUA).

Vanhouttea leonii: BRAZIL. **Minas Gerais:** *Caiafa 5* (VIC); *Hatschbach & J. M. Silva 55446* (G, MBM).

Vanhouttea pendula: BRAZIL. **Espírito Santo:** *Souza et al. 23735* (ESA). **Minas Gerais:** *Caiafa & M. L. Batista 173* (VIC); *Hatschbach, M. Hatschbach & J. M. Silva 55448* (G, MBM, NY, Z).

A PHYTOGEOGRAPHIC ANALYSIS OF ARACEAE OF CABO CORRIENTES (CHOCÓ, COLOMBIA) AND COMPARABLE LOWLAND TROPICAL AMERICAN FLORAS[1]

Marcela Mora,[2] Rodrigo Bernal,[2] Thomas Croat,[3] and Jorge Jácome[2]

Abstract

We studied the Araceae of the Cabo Corrientes region on the Pacific Coast of Colombia and compared its aroid flora with those of La Selva (Costa Rica), Barro Colorado Island (Panama), Bajo Calima (Colombia), Río Palenque (Ecuador), and Iquitos (Peru). We found 114 native species in 14 genera at Cabo Corrientes; the largest genera were *Anthurium* (38 species), and *Philodendron* (36), which together accounted for 65% of the species. Seventy-four percent of the species were exclusively epiphytic or hemiepiphytic. Most of the epiphytic species belonged to the genera *Anthurium*, *Philodendron*, *Rhodospatha*, *Syngonium*, *Monstera*, and *Stenospermation*, the latter three containing exclusively epiphytic or hemiepiphytic species. The flora of Araceae of Cabo Corrientes was most similar to that of La Selva, Barro Colorado Island, and Bajo Calima; similarity with Río Palenque was low. Our findings support Lellinger's view that the Chocó biogeographic region extends to the Nicaragua-Costa Rica border and is divided into a northern and a southern flora.

Key words: Araceae, aroids, Chocó biogeographic region, Colombia, species richness, tropical rainforest.

Resumen

Estudiamos la flora de Araceae de la región de Cabo Corrientes en la Costa Pacífica de Colombia y la comparamos con la flora de aráceas de La Selva (Costa Rica), La Isla de Barro Colorado (Panamá), Bajo Calima (Colombia), Río Palenque (Ecuador) e Iquitos (Peru). En Cabo Corrientes encontramos 114 especies nativas distribuidas en 14 géneros; los géneros más grandes fueron *Anthurium* (38 especies) y *Philodendron* (36), los cuales comprendieron 65% del total de especies. Setenta y cuatro por ciento de las especies fueron exclusivamente epífitas o hemiepífitas. La mayoría de especies epífitas pertenecieron a los géneros *Anthurium*, *Philodendron*, *Rhodospatha*, *Syngonium*, *Monstera*, y *Stenospermation*, siendo los últimos tres géneros exclusivamente epífitos o hemiepífitos. La flora de Araceae de Cabo Corrientes fue más similar con la de La Selva, La Isla de Barro Colorado y Bajo Calima; la similaridad con Río Palenque fue baja. Nuestros resultados coinciden con los de Lellinger que señalan que la región del Chocó biogeografico se extiende hasta la frontera de Costa Rica con Nicaragua y está dividida en una flora norteña y una flora sureña.

Colombia is probably the world's richest, but most poorly known, country for Araceae in South America (Croat, 1992). Colombia's biodiversity, well documented for other groups of organisms (e.g., McNeely et al., 1990; Henderson et al., 1995), is due to the complex mountain system of the country and its location on the crossroads between North and South America. Croat (1992) has suggested that the richest area for Araceae in the country is the Pacific slope of the Andes and the adjacent wet lowlands. This area comprises most of the Chocó biogeographic region, which, as currently defined, stretches from the western slopes of the Andes of Colombia and Ecuador to the Pacific Ocean and from eastern Panama to central coastal Ecuador (Gentry, 1982). The Andean mountains have effectively isolated this region for millions of years, resulting in a high degree of endemism for plants and animals (Gentry, 1993). This fact, coupled with a rainfall that exceeds five meters per year in many areas (Gentry, 1986) and the absence of a long dry season, cause the Pacific lowlands to be an amazing expression of aroid diversity.

The aroid flora has been extensively documented in only one locality in the Pacific lowlands of Colombia (Bajo Calima) (Bay, 1996), although a preliminary survey of another lowland locality (Bahia Solano) has

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been published (Croat, 1992). This paper presents the results of a detailed study of Araceae at a second lowland locality, the Cabo Corrientes area, located on the Pacific coast in the Department of Chocó. We compare the aroid flora of Cabo Corrientes with those of other localities in southern Central America and northern South America and discuss the affinities of the biogeographic Chocó flora.

Materials and Methods

Study site

The study was centered at El Amargal Biological Station, located on the Pacific coast of Colombia 11 km north of Cabo Corrientes. The Cabo Corrientes area is a small peninsula in the Department of Chocó, at the southern end of the coastal Serranía del Baudó. The peninsula is 15 km long and ca. 6 km wide and ranges in elevation from sea level to about 120 m; its terrain is deeply dissected by numerous creeks and small rivers, resulting in an abrupt topography of hills and ravines covered by scarcely disturbed tropical rain forest. The total area of the peninsula is ca. 8000 ha; our sampling covered ca. 2.5 km from the coastline to the east, thus including a total area of ca. 4000 ha.

Collections and comparisons

We collected Araceae at El Amargal from July to September 1998, January to March 1999, and June 2000. Specimens were collected near the visitors' house at the Biological Station, along the trail to the nearby village of Arusí, along the Arusicito river ca. 2 km east of the Station, and at the southern end of the peninsula near Cabo Corrientes. Canopy plants were collected by using tree climbing equipment. Specimens were identified at COL and MO and all identifications were confirmed by Thomas Croat (COL) and/or Michael Grayum (MO).

We compared the aroid flora of Cabo Corrientes with available treatments of aroid floras for five localities: La Selva Biological Station in Costa Rica (Croat & Grayum in Wilbur et al., 1994); Barro Colorado Island (BCI) in Panama (Croat, 1978); Bajo Calima on the Pacific lowlands of Colombia (Bay, 1996); Río Palenque on the coastal lowlands of Ecuador (Dodson & Gentry, 1978, complemented with more recent information, Grayum, 1996); and the Iquitos Reserves in Amazonian Peru (Vásquez, 1997). Information for all localities was complemented with more recent data from the W³ TROPICOS database (2006) at the Missouri Botanical Garden. The complete data set for all localities is available upon request from the first author.

Data analysis

We compared the aroid floras of all pairs of localities using Sørensen's index (Mueller-Dombois & Ellenberg, 1974). For all localities, we excluded from the analysis those species that were introduced and we assumed that all unidentified species were not shared between localities. Thus, our similarity index for any two localities will slightly underestimate similarity if some of the excluded species prove to be shared.

Results

Species diversity

At Cabo Corrientes we found 114 native species of Araceae belonging to 14 genera and two introduced species (Appendix 1). The largest genera were *Anthurium* (38 species) and *Philodendron* (36 species). Together both genera comprise 65% of the local aroid flora. Nine of the species were new records for South America. Twenty-one species (19%), two subspecies, and one variety were new to science (Appendix 1). Of particular interest is the finding of a new subspecies of *Anthurium eminens*, a species so far known only from the Amazon basin.

The pooled data for the six localities gave a total number of 362 species. Only two of the species, *Philodendron inaequilaterum* and *Syngonium podophyllum*, were shared by the six localities; 267 species occurred only at one locality, 41 of them at Cabo Corrientes. The species-richest area was Bajo Calima, followed by Cabo Corrientes and La Selva (Table 1). The largest genera for the pooled floras were also *Anthurium* and *Philodendron*. In all cases *Philodendron* was predominant, except at Cabo Corrientes and Bajo Calima, where *Anthurium* surpassed *Philodendron* by three and two species, respectively. The overall predominance of *Philodendron* over *Anthurium* agrees with Croat's (1994) statement that *Philodendron* is much more abundant at lower elevations than *Anthurium*.

All similarity indices between localities were low (Table 2). Similarities in species richness of Río Palenque and Iquitos with the other localities were the lowest. The highest similarity between two localities was between La Selva and BCI and between La Selva and Cabo Corrientes, although these figures were not much different from the similarity indices of Cabo Corrientes with Bajo Calima and BCI. In contrast, similarity of Bajo Calima with any of these localities, except with Cabo Corrientes, was low.

Generic diversity

Of 19 genera composing the pooled floras, most (11) were shared by all six localities, whereas only a few

Table 1. Generic and specific richness of native Araceae in six neotropical lowland localities.

	Anthurium	*Caladium*	*Chlorospatha*	*Dieffenbachia*	*Dracontium*	*Heteropsis*	*Homalomena*	*Monstera*	*Montrichardia* Crueg.	*Philodendron*	*Pistia* L.	*Rhodospatha*	*Schismatoglottis* Zoll. & Moritzi	*Spathiphyllum*	*Stenospermation*	*Syngonium*	*Urospatha* Schott	*Xanthosoma*	Total
La Selva	25	1	0	7	1	1	1	10	0	30	0	2	0	5	2	7	1	4	97
Barro Colorado Island	13	1	0	3	1	0	1	3	1	17	1	2	0	2	1	2	0	3	51
Cabo Corrientes	38	1	2	4	1	1	3	6	0	36	0	5	0	4	4	7	0	2	114
Bajo Calima	49	2	1	3	1	0	1	5	0	47	0	3	0	2	14	3	0	4	135
Río Palenque	14	1	2	2	0	1	1	4	0	19	0	2	0	1	1	4	0	1	53
Iquitos	20	1	0	8	1	4	2	6	1	28	1	1	1	1	1	1	1	2	80

(5) occurred at only one or two localities (Table 1). The number of genera at Iquitos (17) was higher than that of all other localities (either 13 or 14 genera). *Chlorospatha* was the only genus present at the two Colombian sites and at the one in Ecuador, but lacking at the other localities.

GROWTH HABITS

The aroids of Cabo Corrientes are terrestrial, epiphytic, or hemiepiphytic (Table 3). Of the total number of species, 33 (28%) were true epiphytes, 52 (44%) were true hemiepiphytes, 29 (26%) were terrestrial, and two (2%) were either hemiepiphytes or terrestrial. Of the 14 native genera found at the study site, seven were exclusively terrestrial and four were totally epiphytic (true epiphytes or hemiepiphytes). The only genus that showed all three different habit types was *Anthurium*.

USES

Five of the native species are used locally by African-Colombian people for medicine, construction, or magical-religious purposes. Leaves of *Anthurium trilobum* ("tres dedos"), *Anthurium panamense* ("hoja seca"), and *Dracontium spruceanum* are used for treating snake bite. The aerial roots of *Heteropsis oblongifolia* ("piquigua") are used as cords for binding house beams and are reputed to be the best binding material in the region. As a consequence of pressure on this resource, populations of *Heteropsis* are now severely depleted. Live plants of *Dieffenbachia longispatha* ("hoja de chucha") are planted at one of the front corners of dwellings as a protection against witchcraft. Additionally, two common, well-known, introduced species, *Xanthosoma sagittifolium* ("otó") and *Colocasia esculenta* ("achín") are cultivated in the nearby village of Arusí. Their starch-rich tubers are used for human and animal food.

DISCUSSION

The number of aroid species in the Cabo Corrientes area is higher than the total number of species listed for this family by Forero and Gentry (1989) in the whole Chocó Department, even though their list includes the western slopes of the Cordillera Occidental. This fact stresses the poor knowledge of the aroid flora of the Chocó Department. Thus, for example, Grayum (1996) noted a marked absence of *Philodendron* subg. *Pteromischum* (Schott) Mayo in this department and suggested that there might be a discontinuity of distribution of the group in this area. However, at Cabo Corrientes we found ten species of this subgenus, which represents 45% of all the species of this group known in Colombia. Of these ten species, *Philodendron croatii* and *P. rayanum* are new records for the South American flora.

The poor knowledge of the Araceae of this region reflects both the incomplete exploration of the area and the bias of recent inventories, most of which have studied forest composition in terms of trees, ignoring the diversity represented in other growth forms, as pointed out by Galeano et al. (1998b). The latter authors found that at Cabo Corrientes and nearby areas the Araceae were by far the most species-rich family, accounting for 10.3% of all vascular plants. Not surprisingly, the biogeographic Chocó has been

Table 2. Sørensen's index matrix for paired comparisons of aroid species richness at six neotropical localities.

Locality	La Selva	BCI	Cabo Corrientes	Bajo Calima	Río Palenque	Iquitos
La Selva	1	0.392	0.391	0.216	0.160	0.124
BCI	0.392	1	0.329	0.150	0.154	0.183
Cabo Corrientes	0.391	0.329	1	0.355	0.205	0.114
Bajo Calima	0.216	0.150	0.355	1	0.191	0.056
Río Palenque	0.160	0.154	0.205	0.191	1	0.105
Iquitos	0.124	0.183	0.114	0.056	0.105	1

pointed to as the world's richest region for Araceae (Croat, 1992).

The richness of Araceae in this region is probably due to a combination of a high level of endemism and the great affinity of its flora to that of southern Central America. The high level of endemism in the Chocó, estimated for all plant groups to be near 20% (Gentry, 1982), is evidenced for the Araceae by the large number of new species found in the two detailed studies so far carried out in the lowlands (Bay, 1996; Croat & Mora, 2004; Croat et al., 2006): 37% of the 205 species in the pooled floras of Bajo Calima and Cabo Corrientes were new to science. The fact that most of these species have not been found before in better-explored Costa Rica or Panama suggests that they may be endemic to the Chocó.

The affinity of the Chocó flora with that of southern Central America has been shown by many authors (e.g., Gentry, 1982; Croat, 1992; Galeano, 1992; Bernal & Galeano, 1993; Grayum, 1996; Galeano et al., 1998a). In fact, 73% of the aroids of Cabo Corrientes are also found in Central America, and 48% of all aroid species are known only from Central America and the Chocó region (Mora et al., unpublished data). Sørensen's similarity indices for the six aroid floras (Table 2) further stress this affinity: the similarity of Cabo Corrientes with La Selva and BCI is comparable to that between La Selva and BCI. Interestingly, Río Palenque and Bajo Calima seem to have a lower affinity with Central America. In fact, the similarity indices between La Selva and other sites to the south showed an abrupt reduction at Bajo Calima, despite its closeness to Cabo Corrientes. On the other hand, Río Palenque showed a low similarity with all of the above-mentioned localities, despite its purported affinity to the Chocó biogeographic region (Gentry, 1982, 1986); the similarity indices between Río Palenque and other localities were comparable to those of Iquitos.

Table 3. Growth habit of the Araceae of Cabo Corrientes, Chocó, Colombia. All species within each genus have that particular growth habit unless otherwise noted with the number of species in parenthesis. One species of *Philodendron* and one of *Rhodospatha* are either terrestrial or hemiepiphitic.

Terrestrial	Hemiepiphytes	Epiphytes
Anthurium (8)	*Anthurium* (1)	*Anthurium* (29)
Caladium	*Heteropsis*	*Stenospermation*
Chlorospatha	*Monstera*	
Dieffenbachia	*Philodendron* (32)	
Dracontium	*Rhodospatha* (6)	
Homalomena	*Syngonium*	
Philodendron (1)		
Rhodospatha (1)		
Spathiphyllum		
Xanthosoma		

The strong affinity of the Cabo Corrientes aroid flora with that of southern Central America suggests that the northern limit of the Chocó biogeographic region does not lie near the Panama-Colombia border, as suggested by Gentry (1982, 1986, 1993) and as currently recognized, but the region may extend north to the border between Nicaragua and Costa Rica, as initially stated by Lellinger and de La Sota (1978). On the other hand, the dissimilarity of Bajo Calima and Río Palenque with Central America, in terms of aroids, supports Lellinger's (1975) distinction, based on ferns, of a northern and a southern Chocó flora. According to Lellinger, the division between both fern floras would be near the southern boundary of the Chocó Department (i.e., near Bajo Calima). If Bajo Calima indeed lies near the contact area between Lellinger's northern and southern Chocó floras, this might perhaps explain its extreme endemism in aroids, indicated by the fact that 54 of the species found by Bay (1996) were new to science. High endemism had already been noted by Gentry (1982) for the Bajo Calima and neighboring areas in the Valle Department, as well as for Río Palenque. The low similarity between the aroid floras of the latter localities suggests that endemism in the southern Chocó flora is not uniformly distributed, and that at least two areas of endemism may exist. Unfortunately, the poor floristic knowledge of the lowlands in the intervening Cauca and Nariño Departments of Colombia currently prevents any further analysis.

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Appendix 1. Checklist of the Araceae of Cabo Corrientes, Colombia, and growth habits of the species. E, epiphytic; H, hemiepiphytic; T, terrestrial. Genera are in bold; taxa marked with solid circles are new species (Croat & Mora, 2004) and the two marked with an asterisk are introduced.

Taxon	Habit	Voucher
Anthurium		
acutangulum Engl.	E	Mora 10 (COL, MO), Mora & Croat 281 (COL, MO)
acutibacca Croat & M. M. Mora•	E	Mora 39 (COL, MO), Jácome 335 (COL), Mora & Croat 363 (COL, MO)
amargalense Croat & M. M. Mora•	E	Mora & Croat 385 (COL, MO)
arusiense Croat & M. M. Mora•	E	Mora & Croat 352 (COL, MO), Jácome 414 (COL)
brownii Mast.	E	Mora 32 (COL, MO), Mora & Croat 323 (COL, MO)
cogolloanum Croat & M. M. Mora•	E	Mora 64 (COL), Mora & Croat 393 (COL, MO)
colonense Croat	E	Mora & Croat 313 (COL, MO)
cucullispathum Croat	E	Mora 76 (COL, MO), Mora & Croat 316 (COL, MO)
cuspidatum Matuda	T	Mora & Croat (COL)
debilis Croat & D. C. Bay•	T	Mora 7 (COL)
dwyeri Croat	E	Mora & Croat 357 (COL, MO)
eminens Schott ssp. *longispadix* Croat & M. M. Mora•	E	Mora 33 (COL, MO), Mora & Croat 331 (COL, MO)
formosum Schott	T	Mora 62 (COL, MO), Mora & Croat 347 (COL, MO)
friedrichsthalii Schott	E	Mora 24 (COL, MO), Mora & Croat 318 (COL, MO)
galeanoae Croat & M. M. Mora•	E	Mora & Croat 329 (COL, MO)
grandicataphyllum Croat & M. M. Mora•	E	Mora 66 (COL, MO), Mora & Croat 376 (COL, MO)
hacumense Engl.	E	Jácome 224 (COL)
hodgei Croat, M. M. Mora & Oberle•	E	Mora & Croat 391 (COL, MO)
kunthii Poepp.	E	Jácome 419 (COL)
lancifolium Schott	T	Mora 4 (COL, MO), Mora & Croat 301 (COL)
michelii Guillaumin	E	Mora 45 (COL, MO), Mora & Croat 375 (COL, MO)
morae Croat•	E	Mora 31 (COL, MO), Mora & Croat 343 (COL)
obtusilobum Schott	E	Mora 41 (COL, MO), Mora & Croat 382 (COL, MO)
obtusum (Engl.) Grayum	E	Mora 30 (COL), Mora & Croat 349 (COL, MO)
pallidicaudex Croat & M. M. Mora•	T	Mora 43 (COL, MO), Mora & Croat 344 (COL, MO)
paludosum Engl.	E	Mora 23 (COL, MO), Mora & Croat 365 (COL, MO)
panamense Croat	E	Mora 14 (COL, MO), Mora & Croat 276
promininerve Croat & M. M. Mora•	T	Mora 28 (COL, MO), Mora & Croat 332 (COL, MO)
propinquum Sodiro	T	Mora 48 (COL, MO), Mora & Croat 315 (COL, MO)
ramonense Engl. ex K. Krause	E	Mora & Croat 314 (COL)
ravenii Croat & R. A. Baker	E	Mora 32 (COL), Mora & Croat 277 (COL, MO)
rotundistigmatum Croat	E	Mora 55 (COL, MO), Mora & Croat 374
salvinii Hemsl.	E	Mora & Croat 356 (COL, MO)
trilobum Hort. Linden ex André	E	Mora 18 (COL, MO), Mora & Croat 312 (COL, MO)
variilobum Croat & M. M. Mora•	T	Mora 11 (COL, MO), Mora & Croat 350 (COL, MO)
wurocqueanum Moore	H	Mora 47 (COL, MO), Mora & Croat 295 (COL, MO)
sp. indet. 1 [sect. *Porphyrochitonium* Schott]	E	Mora & Croat 363 (COL, MO)
sp. indet. 2 [sect. *Digittinervium* Sodiro]	E	Mora & Croat 385 (COL, MO)
Caladium		
bicolor (Aiton) Vent.	T	Mora 154 (COL)
Chlorospatha		
kolbii Engl.	T	Mora 50 (COL, MO), Mora & Croat 345 (COL, MO)
mirabilis (Mast.) Madison	T	Mora 56 (COL), Mora & Croat 304 (COL, MO)
Colocasia		
esculenta (L.) Schott*	T	Mora & Croat 392 (COL)
Dieffenbachia		
davidsei Croat & Grayum•	T	Jácome 356 (COL), Mora & Croat 303 (COL, MO)
longispatha Engl. & K. Krause	T	Mora 72 (COL), Mora & Croat 394 (COL, MO)
nitidipetiolata Croat & Grayum•	T	Mora 49 (COL), Mora & Croat 270 (COL, MO)
tonduzii Croat & Grayum	T	Mora 51 (COL), Mora & Croat 310 (COL, MO)
Dracontium		
spruceanum (Schott) G. H Zhu	T	Jácome 399 (COL), Mora & Croat 335 (COL, MO)

Appendix 1. Continued.

Taxon	Habit	Voucher
Heteropsis		
oblongifolia Kunth	H	Jácome 390 (COL), 401 (MO)
Homalomena		
erythropus (Mart. ex Schott) Engl. ssp. *allenii* Croat•	T	Mora 38 (COL), Mora & Croat 271 (COL)
peltata Mast.	T	Mora 77 (COL, MO), Mora & Croat 301 (COL, MO)
wendlandii Schott	T	Mora 75 (COL, MO), Mora & Croat 336 (COL, MO)
Monstera		
adansonii Schott	H	Mora & Croat 324 (COL, MO), Jácome 423 (COL, MO)
var. *laniata* (Schott) Madison	H	Mora 65 (COL), Mora & Croat 324 (COL, MO)
amargalensis Croat & M. M. Mora•	H	Mora & Croat 324 (COL, MO), Jácome 423 (COL, MO)
dubia (Kunth) Engl. & K. Krause	H	Mora 54 (COL, MO), Mora & Croat 340 (COL, MO)
minima Madison	H	Jácome 280 (COL)
obliqua Miq.	H	Mora 53 (COL, MO)
pittieri Engler	H	Jácome 280 (COL)
pinnatipartita Schott	H	Mora 42 (COL, MO), Mora & Croat 306 (COL, MO)
spruceana (Schott) Engl.	H	Mora 26 (COL), Mora & Croat 265 (COL, MO)
Philodendron		
alliodorum Croat & Grayum	H	Jácome 226 (COL), Mora & Croat 285 (COL, MO)
amargalense Croat & M. M. Mora•	H	Mora & Croat 280 (COL, MO), Mora & Croat 320 (COL, MO)
angustilobum Croat & Grayum	H	Mora 60 (COL, MO)
bakeri Croat & Grayum	H	Jácome 228 (COL)
croatii Grayum	H	Jácome 369 (COL)
ensifolium Croat & Grayum	H	Jácome 337 (COL)
fragrantissimum (Hook.) Kunth	H	Mora 37 (COL)
grandipes K. Krause	T	Mora 27 (COL, MO); Mora & Croat 272 (COL)
grayumii Croat	H	Mora 16 (COL, MO), Mora & Croat 264 (COL, MO)
hebetatum Croat	H, T	Mora 67 (COL, MO), Mora & Croat 325 (COL, MO)
hederaceum (Jacq.) Schott	H	Mora 76 (COL), Mora & Croat 319 (COL, MO)
heleniae Croat	H	Mora 36 (COL, MO), Mora & Croat 321 (COL, MO)
ichthyoderma Croat & Grayum	T	Mora 74 (COL), Mora & Croat (COL)
immixtum Croat	H	Mora & Croat 354A (COL, MO)
inaequilaterum Liebm.	T	Jácome 263 (COL)
jodavisianum G. S. Bunting	H	Mora 3 (COL, MO), Mora & Croat 339 (COL, MO)
laticiferum Croat & M. M. Mora•	H	Mora 9 (COL, MO)
ligulatum Schott	H	Mora 17 (COL, MO), Mora & Croat 266 (COL, MO)
longipedunculatum Croat & M. M. Mora•	H	Mora 61 (COL)
opacum Croat & Grayum	H	Mora 71 (COL, MO), Mora & Croat 359 (COL, MO)
panamense K. Krause	H	Mora & Croat 369 (COL, MO)
platypetiolatum Madison	H	Mora 29 (COL, MO), Mora & Croat 322 (COL, MO)
rayanum Croat & Grayum	H	Jácome 322 (COL)
rhodoaxis G. S. Bunting ssp. *lewisii* Croat & Grayum	H	Jácome 243 (COL), Mora & Croat 292 (COL, MO)
roseocataphyllum Croat & M. M. Mora•	H	Mora 63 (COL, MO), Mora & Croat 384 (COL, MO)
sagittifolium Liebm.	H	Jácome 238 (COL), Mora & Croat 280 (COL, MO)
scalarinerve Croat & Grayum	H	Mora 12 (COL, MO), Mora & Croat 277 (COL, MO)
senatocarpium Madison	H	Mora & Croat 326 (COL, MO)
strictum G. S. Bunting	T	Mora 59 (COL)
subhastatum Engl.	H	Mora & Croat 355 (COL, MO)
sulcatum K. Krause	H	Jácome 355 (COL)
sulcicaule Croat & Grayum	H	Jácome 219 (COL)
tenue K. Koch & Augustin	H	Mora 57 (COL), Mora & Croat 348 (COL, MO)
tripartitum (Jacq.) Schott	H	Mora 127 (COL), Mora & Croat 316 (COL, MO)
sp. indet. 1	H	Jácome 262 (COL)
sp. indet. 2	H	Mora 68 (COL), Mora & Croat 327 (COL)

Appendix 1. Continued.

Taxon	Habit	Voucher
Rhodospatha		
brachypoda G. S. Bunting	H	Mora & Croat 361 (COL)
monsalveae Croat & D. C. Bay*	H	Mora 40 (COL)
moritziana Schott	H, T	Mora 1 (COL, MO), Mora & Croat 282, 287 (COL, MO)
pellucida Croat & Grayum	H	Jácome 426 (COL)
wendlandii Schott	H	Jácome 248 (COL)
sp. indet. 1	H	Mora & Croat 299 (COL)
Spathiphyllum		
dressleri Croat & F. Cardona*	T	Mora & Croat 366 (COL)
friedrichsthalii Schott	T	Mora 25 (COL), 91 (COL, MO), Mora & Croat 387 (COL, MO)
phryniifolium Schott	T	Mora 15 (COL), Mora & Croat 328 (COL, MO)
laeve Engl.	T	Mora 5 (COL, MO), Mora & Croat 311 (COL, MO)
Stenospermation		
angustifolium Hemsl.	E	Mora 20 (COL, MO), Mora & Croat (COL, MO)
latifolium Engl.	E	Mora & Croat 263 (COL)
multiovulatum (Engl.) N. E. Br.	E	Mora 13 (COL), Mora & Croat 279 (COL, MO)
robustum Engl.	E	Mora 34 (COL), Mora & Croat 275 (COL, MO)
Syngonium		
erythrophyllum Birdsey ex G. S. Bunting	H	Mora 69 (COL), Mora & Croat 290 (COL, MO)
macrophyllum Engl.	H	Mora 21 (COL), Mora & Croat 368 (COL)
chocoanum Croat	H	Mora 7 (COL, MO), Jácome 380 (COL)
podophyllum Schott	H	Mora & Croat 341 (COL, MO)
triphyllum Birdsey ex Croat	H	Mora & Croat 334 (COL, MO)
Xanthosoma		
daguense Engl.	T	Mora 19 (COL, MO), Mora & Croat 268 (COL, MO)
var. *amargalense* Croat & M. M. Mora*	T	Mora & Croat 300 (COL, MO), Jácome 400 (COL)
sagittifolium (L.) Schott & Endl.	T	No voucher (pers. comm., Croat)

SCIENCE WITH A SOCIAL CONSCIENCE: DIGGING FOR DINOSAURS AND HELPING CHILDREN IN THE LAND THAT TIME FORGOT

David W. Krause[1]

Madagascar has been good to us. In 1993, I led a reconnaissance expedition in search of Cretaceous dinosaurs, mammals, and other vertebrate animals to this, the fourth-largest island in the world. Not in my wildest dreams did I anticipate the fossil riches that we would find on that expedition, or on the seven field campaigns since. Many of our discoveries are documented in an article in this volume (see pp. 178–208).

What we also found, however, were some of the most abandoned and destitute people on the planet. Many of Madagascar's citizens, particularly in rural areas, do not know how to read or write and have never been seen by a doctor or dentist. Malnutrition is ubiquitous. Children, who are otherwise rail thin, have abdomens that are visibly distended, largely a result of protein deficiency but oftentimes also owing to endemic parasites that inhabit, multiply within, and thus enlarge spleens and livers. Malaria is rampant. Upper respiratory, diarrheal, and dental infections are common and, owing to the lack of access to basic hygiene and antibiotics, all too frequently fatal.

These same Malagasy villagers welcomed us into their communities, directed us to productive field areas, and helped us carry massive plaster jackets containing fossil specimens over kilometers of rough terrain to waiting vehicles. With a desire to repay them for their many kindnesses, we asked what we could do. They humbly requested a school for their children. It was a "no-brainer" when we learned we could get things started by hiring a teacher for only US$500/year.

In 1998 my colleagues and I formalized and expanded our efforts by establishing the Madagascar Ankizy Fund (MAF). The primary mission of MAF is to provide education and health care to children ("ankizy" in the Malagasy language) living in remote areas of the island nation, which currently has a population of 18 million. To date, MAF can claim the following successes: (1) the building and inauguration of two elementary schools, one of them in our field area in northwestern Madagascar (Fig. 1), the other in a rainforest in the east (two more are in the planning stages); (2) establishment of annual health care clinics in remote areas, staffed largely by Stony Brook University personnel; (3) drilling of several wells and initiation of a water disinfection program; (4) initiation of an arts and crafts industry in a village starving because the primary occupation, woodcutting (charcoal production), is no longer feasible since the forest has been depleted; (5) renovation of an orphanage in the city of Mahajanga; (6) initiation of community-wide education programs in nutrition, hygiene, and sexual health; (7) establishment of sister-institution status between the Stony Brook University School of Dental Medicine and the only dental school in Madagascar; and (8) initiation of a program through which used and surplus hospital equipment and supplies are shipped from hospitals in the U.S.A. to those in Madagascar.

Funding for MAF projects is derived from several sources: grants from organizations such as Rotary International, various administrative units at Stony Brook University, private individuals, and American children who conduct fundraisers in their schools. The latter is particularly gratifying because it has a reciprocal effect: children in Madagascar benefit from the relative wealth of children in the U.S.A. while the latter learn a great deal about the country and people of Madagascar. Importantly, American schoolchildren have the additional benefit of discovering that they can make a meaningful difference in the lives of much less fortunate children.

Why am I writing this article? Partly because the editors of this volume kindly invited me to do so but primarily for two reasons: (1) to seek assistance for MAF projects by directing readers to visit the MAF

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Figure 1. Dr. David W. Krause (left) with teachers and children at inauguration of the Berivotra Elementary School, built by the Madagascar Ankizy Fund. Photo credit: Ashutosh Kaushesh.

website at www.ankizy.org, and (2) to encourage and hopefully inspire other researchers working in developing countries to initiate similar efforts. As scientists, both professionals and students, we have collected and studied literally thousands of specimens from Madagascar, and our careers have been advanced immeasurably as a result. This is simply our way of giving back to a country that has given us so much.

MAF is administered by the Stony Brook Foundation, a 501(c)3 not-for-profit education corporation established by Stony Brook University to receive and manage philanthropic contributions.

Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 2005

	Vascular plants	Bryophyte	Totals
Acquisitions of Specimens			
Staff Collections	23,786	1,820	25,606
Purchase	12,550	0	12,550
Exchange	19,142	3,285	22,427
Gifts	15,910	669	16,579
Total acquisitions	71,388	5,774	77,162
Mountings			
Newly mounted at MO	96,089	16,033	112,122
Specimens mounted when acquired	0	0	0
Total mountings	96,089	16,033	112,122
Repairs			
Specimens repaired	20,975	0	20,975
Specimens stamped	1,359	0	1,359
Total repairs	22,334	0	22,334
Specimens sent			
On exchange	24,293	6,455	30,748
As gifts	18,111	1,238	19,349
Total	42,404	7,693	50,097
Loans sent			
Total transactions	295	34	329
Total specimens	25,894	1,424	27,318
To US institutions			
Transactions	153	16	169
Specimens	13,620	367	13,987
To foreign institutions			
Transactions	142	18	160
Specimens	12,274	1,057	13,331
To student investigators			
Transactions	53	5	58
Specimens	5,866	440	6,306
To professional investigators			
Transactions	242	29	271
Specimens	20,028	984	21,012
Loans received			
Transactions	160	68	228
Specimens	13,727	7,247	20,974
	From U.S.A.	From abroad	Total
Visitors	237	109	346

Ann. Missouri Bot. Gard. 93: 369–370. Published on 23 August 2006.

The Garden's herbarium is closely associated with its database management system, TROPICOS (see www.tropicos.org). The charts below summarize some of the statistics from TROPICOS both for the calendar year 2005 and year-end totals. At the end of 2005 the Garden's herbarium held 5,749,641 numbered sheets: 5,283,152 vascular plants and 466,489 bryophytes.

TROPICOS RECORD SUMMARY

Calendar year 2005	Vascular Plants	Bryophytes	Totals
Specimens	525,672	13,742	539,414
Names	18,163	304	18,467
Synonyms	6,137	2,965	9,102
Distributions	12,965	251	13,216
Types	6,299	101	6,400
Bibliography	3,511	2,800	6,311

Year end 2005 Totals	Vascular Plants	Bryophytes	Totals
Specimens	2,720,537	206,922	2,927,459
Names	879,290	108,407	987,697
Synonyms	432,007	74,238	506,245
Distributions	877,120	43,770	920,890
Types	322,977	9,823	332,800
Bibliography	76,074	31,005	107,079

In TROPICOS, taxonomic synonymy is always linked to a reference in Bibliography and directly with at least two records in Names, i.e. the synonym and the correct name according to the reference. Additional nomenclatural synonymy may be derived from these direct links, e.g. all other combinations of a basionym treated as a synonym of a given name are also synonyms of that name.

—James C. Solomon and Robert E. Magill

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Cover illustration. *Capparis sicula* subsp. *mesopotamica* Inocencio, D. Rivera, Obón & Alcaraz, drawn by Jose-Antonio Barreña.

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A TAXONOMIC REVISION OF CARIBBEAN *ADIANTOPSIS* (PTERIDACEAE)[1,2]

Michael S. Barker[3,4] *and R. James Hickey*[3]

Abstract

Adiantopsis Fée (Pteridaceae) is a relatively unstudied tropical cheilanthoid fern genus. In the present work, we evaluated the taxonomy and relationships among Caribbean *Adiantopsis* by examining 136 characters from approximately 500 herbarium specimens. This study identified nine Caribbean *Adiantopsis* species, three of which are newly described (*A. parvisegmenta*, *A. pentagona*, and *A. vincentii*). Additionally, an intriguing pattern of morphological and reticulate evolution was revealed by the analyses. *Adiantopsis* consists of three different laminar morphologies: palmate, pedate, and pinnate. The two pedate taxa are hypothesized to be fertile allotetraploid derivatives of the palmate *A. radiata* (L.) Fée and two different pinnate taxa. In this regard they parallel the origin of the South American *A.* ×*australopedata* Hickey, M. S. Barker & Ponce. Based on our analyses, it appears that pedate laminar morphologies in *Adiantopsis* independently originated multiple times via hybridization. This study provides testable hypotheses of morphological and reticulate evolution in the genus and presents a novel view of Caribbean *Adiantopsis*.

Key words: *Adiantopsis*, Caribbean flora, cheilanthoid, ferns, monilophytes, Pteridophytes.

Adiantopsis Fée is a cheilanthoid fern genus found throughout tropical America (Tryon & Tryon, 1982) and possibly Africa (Moran & Smith, 2001). A combination of echinate spores, distinct pseudoindusia, adaxial carinae, and unique septate-capitate hairs on the axes and laminar surfaces distinguishes *Adiantopsis* from other cheilanthoids. Historically, the genus was interpreted to include seven species, four of which occur in the Caribbean, predominantly in Cuba and Jamaica (Tryon & Tryon, 1982). In this regional revision, we recognize nine Caribbean species out of an estimated 20 *Adiantopsis* species worldwide. In the Caribbean, *Adiantopsis* is a genus primarily of calcareous forests and cliffs. Six of the nine Caribbean *Adiantopsis* species are limited to narrow ecological niches, such as serpentine soils,

[1] The authors thank the cited curators and institutions for providing specimen loans. M. Vincent and MU deserve thanks for handling loans and making space for our material. J. Budke, K. Heafner, and S. Shaw provided support in the lab. D. Lellinger assisted us with collections and unique nomenclatural information at US. M. Sundue was very helpful upon a visit to NY. We thank W. Harris for assistance with specimen data entry and J. Gastony for reviewing our Latin diagnoses. Comments from W. Hauk, V. Hollowell, J. Mickel, and an anonymous reviewer significantly improved the manuscript. We are also indebted to the Ohio Academic Challenge program, the Botany Department at Miami University, and the Willard Sherman Turrell Herbarium Fund for financial support.

[2] The editors of the *Annals* thank Sophia Balcomb for her editorial contribution to this article.

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and are endemic to small geographic areas of single islands.

Relative to other cheilanthoid genera, a paucity of information exists about *Adiantopsis*. It is one of many small, overlooked tropical genera that have never been examined using formal taxonomic methods. Holttum (1975: 500) recognized this problem nearly 30 years ago, and called for "New total monographs...to reveal the kinds of groups which can be tackled by the methods of biosystematics." Reasons for studying *Adiantopsis* were simply to describe and enumerate the taxa present, and increase our knowledge of this genus. Such knowledge is a prerequisite for future systematic, molecular, and evolutionary research on *Adiantopsis*. Additionally, taxonomic research on *Adiantopsis* provides data for the eventual reorganization of the polyphyletic *Cheilanthes* Sw. (Gastony, unpublished data) into a natural (i.e., monophyletic) classification scheme, something that is not possible without basic research on *Adiantopsis* and other understudied elements of *Cheilanthes*.

Adiantopsis also possesses a striking range of laminar morphology. The laminae may be palmate (radiate), pedate, or pinnate. This range of variation does not occur in many other fern genera, especially ones as small as *Adiantopsis*. However, without a solid taxonomy of the species, understanding the evolution of this variation is not possible. Thus, another reason for studying *Adiantopsis* was to develop and evaluate hypotheses about the origin of these laminar morphologies.

The results presented in this revision are a component of a complete monograph of *Adiantopsis* that is currently in progress. In this publication, a taxonomic revision of the Caribbean *Adiantopsis* taxa is presented; the Central and South American taxa will be included in a future, more comprehensive monograph. Although this taxonomic treatment deals only with the Caribbean species, the discussion of *Adiantopsis* biology in this revision should apply to the entire genus.

Materials and Methods

We examined approximately 500 specimens from the following herbaria for this revision: B, BM, DUKE, F, FI, GH, K, L, MICH, MO, MU, NY, P, UC, and US. In all, 136 characters were scored for each species. For the most part, morphological characters were recorded without disturbing the specimen, and were collected by eye or with a dissecting microscope. An Olympus BH-2 compound light microscope was used to examine microscopic characters. The methodologies for describing characters requiring special preparation are described below.

For length and width measurements, scales of the rhizome, stipe, and rachis were mounted in Hoyer's solution (Anderson, 1954) on a microscope slide. Measurements were made on a compound light microscope. Scales were collected only from specimens with numerous scales, so that specimens would still possess scales for future research.

Guard cell measurements were made with a compound light microscope using prepared laminar tissue. Ultimate divisions were collected from various parts of the frond to avoid any difference in guard cell length attributed to position. The collected laminar tissue was placed into a 30% weight/volume (w/v) NaOH solution for 20 minutes to remove epicuticular wax. To decolorize the tissue, it was taken through an ethanol series of 20%, 50%, 85%, and 100%, and then backward through that series to water. The tissue was kept at each stage of the series for 10 minutes. The decolorized tissue was stained using a modification of Foster's Tannic Acid – Iron Chloride method (Johansen, 1940): decolorized tissue was placed in a 1% w/v aqueous solution of tannic acid for 10 minutes, briefly rinsed in water, and transferred to a 3% w/v aqueous solution of ferric chloride for approximately 30 minutes. The tannic acid and ferric chloride steps were repeated until the cell walls were dark enough to be readily seen. Once the visibility of the cell walls was satisfactory, the tissue was mounted on slides using Hoyer's solution, and guard cell length measurements were made on a compound light microscope.

Sporangia were collected from herbarium specimens using forceps and mounted on a slide with Hoyer's solution. Two measurements were made from collected sporangia: the number of indurated arcus cells, and their height. Data were collected on a compound light microscope.

Spores were collected from herbarium specimens and examined using both Scanning Electron Microscopy (SEM) and light microscopy. Spores for SEM were collected from open sporangia to ensure that the spores were mature and that there were no contaminating spores from other specimens. For counting spore number per sporangium, complete intact sporangia were collected from each specimen. The closed sporangia were collected using fine forceps and transferred to an aluminum SEM stub that was prepared with a double-sided sticky tab and a drop of water. The water allowed the spores to be easily scattered over the surface of the stub and kept the spores on the stub when breaking open intact sporangia. SEM stubs were gold-palladium sputter coated for 90 seconds at 45 milliamps. Spores were examined on a JEOL JSM-T200 SEM at various working distances, voltages, and spot sizes, depending

on the stub. Pictures were taken using an attached Land camera with Polaroid Polapan 55 black and white film. For light microscopy, spores were collected with fine forceps from open sporangia. These spores were mounted on a slide with Hoyer's solution and measured on a compound light microscope.

Data analyses were conducted using SAS (Version 8; SAS, 2000) and OpenOffice.org Calc (Version 1.1; OpenOffice.org, 2003). Guard cell, arcus cell, and spore size data were compared in SAS using one-way ANOVAs with Tukey-Kramer multiple pairwise comparisons (α = 0.05) to identify significantly different values. Ranges, means, modes, and standard deviations for all quantitative characters were calculated using OpenOffice.org Calc. Box plots and histograms for select data sets were constructed using OpenOffice.org Calc.

Character terminology in this revision generally follows Lellinger (2002). One deviation is the scoring of planar shapes; these were characterized using the "Symmetric Plane Figures" guide published by the Systematics Association Committee (1962). Additionally, as *Adiantopsis* possesses complex laminar architectures, terms relating to the pinnae and pinnules have been slightly modified from Lellinger (2002). In taxa that are more than bipinnately compound, the term ultimate division, which is not in Lellinger (2002), is used to describe any portion of the lamina that is not further dissected or compound, regardless of its position. Thus, an ultimate division may be a pinna, a pinnule, or a pinnulet, so long as it is not further divided. When using the term ultimate division to describe these various structures, no homology is implied. Thus, pinnae are still the primary division of the lamina, but when pinna morphology is described it applies only to pinnae that are compound themselves (i.e., bipinnate and more compound species). This same logic applies to pinnules. Thus, all final divisions of the lamina are grouped under ultimate division; divisions that are themselves compound are described using standard positional terms (pinna, pinnule, etc.).

Ecology

Adiantopsis species are ecologically variable. Caribbean *Adiantopsis* frequently occur in moist, forested areas, or on moist rock walls, often in gullies or cave entrances. In South America, many species also prefer moist, forested areas, often occurring near streams or on stream banks, although some South American *Adiantopsis*, such as some elements of *A. chlorophylla* (Sw.) T. Moore, do prefer exposed, rocky habitats. An alkaline substrate appears to be a requisite for many *Adiantopsis* taxa. In the Caribbean, this includes limestone, serpentine, and amphibolite substrates. *Adiantopsis radiata* (L.) Fée may be able to grow in a variety of pH substrates. However, at least one South American species, *A. monticola* (Gardner) T. Moore, prefers acidic substrates. *Adiantopsis* taxa occur from near sea level to as high as 2800 m (Tryon & Stolze, 1989).

Morphology

No previous generic-level description of *Adiantopsis* morphology exists. The following description is the first of its sort for the genus. However, it cannot be considered comprehensive as it only represents data and patterns observable from herbarium specimens and excludes possible Old World members.

Adiantopsis is a genus of generally erect, small to large herbaceous ferns. Among the Caribbean species, the plants (as a function of leaf length) range from small (9.5 cm in *A. asplenioides* Maxon) to medium sized (to 74.0 cm in *A. parvisegmenta* M. S. Barker & Hickey); most individuals are around 20–40 cm long. Larger taxa occur in South America, such as *A. chlorophylla* and *A.* ×*australopedata* Hickey, M. S. Barker & Ponce, that may exceed one and a half meters in length. Most *Adiantopsis* taxa are strict, or stiffly erect. In *A. asplenioides* and *A. paupercula* (Kunze) Fée, the plants are also erect, but the stipes are not as stiff as other taxa. Caribbean *Adiantopsis* taxa are generally smaller than their South American congeners, and less habit variation is observed.

The rhizomes of *Adiantopsis* taxa are all similar. Rhizomes range from erect, to ascending, to decumbent. It is not clear if rhizomes are distinctly subterranean or marginally surficial, but given the amount of soil on most rhizomes they appear to be at least partially hypogeal. In this respect, no difference is observed among taxa. Rhizomes range to 5.9 cm long and 2.3 cm diameter. Persistent, bicolorous scales densely cover the rhizomes (Figure 1A); these may play some role in preventing dessication and/or infection by fungi or bacteria. In all species, a dense tangle of fibrous roots emerges from all sides of the rhizome. Stipes also emerge from all sides of the rhizomes, suggesting a fundamentally radial symmetry (Figure 1A). No positional relationship was observed between the stipes and the roots.

Frond axes in *Adiantopsis* are typically cheilanthoid. They are generally persistent and atropurpureous to atrocastaneous, becoming darker at senescence. *Adiantopsis* axes are also carinate adaxially (Figure 1B). These carinae are in the form of paired, golden ridges raised above the surface of the axis (described as "sclerotic ribs" for putative *Adiantopsis* taxa in Ponce & Morbelli, 1989). Tryon

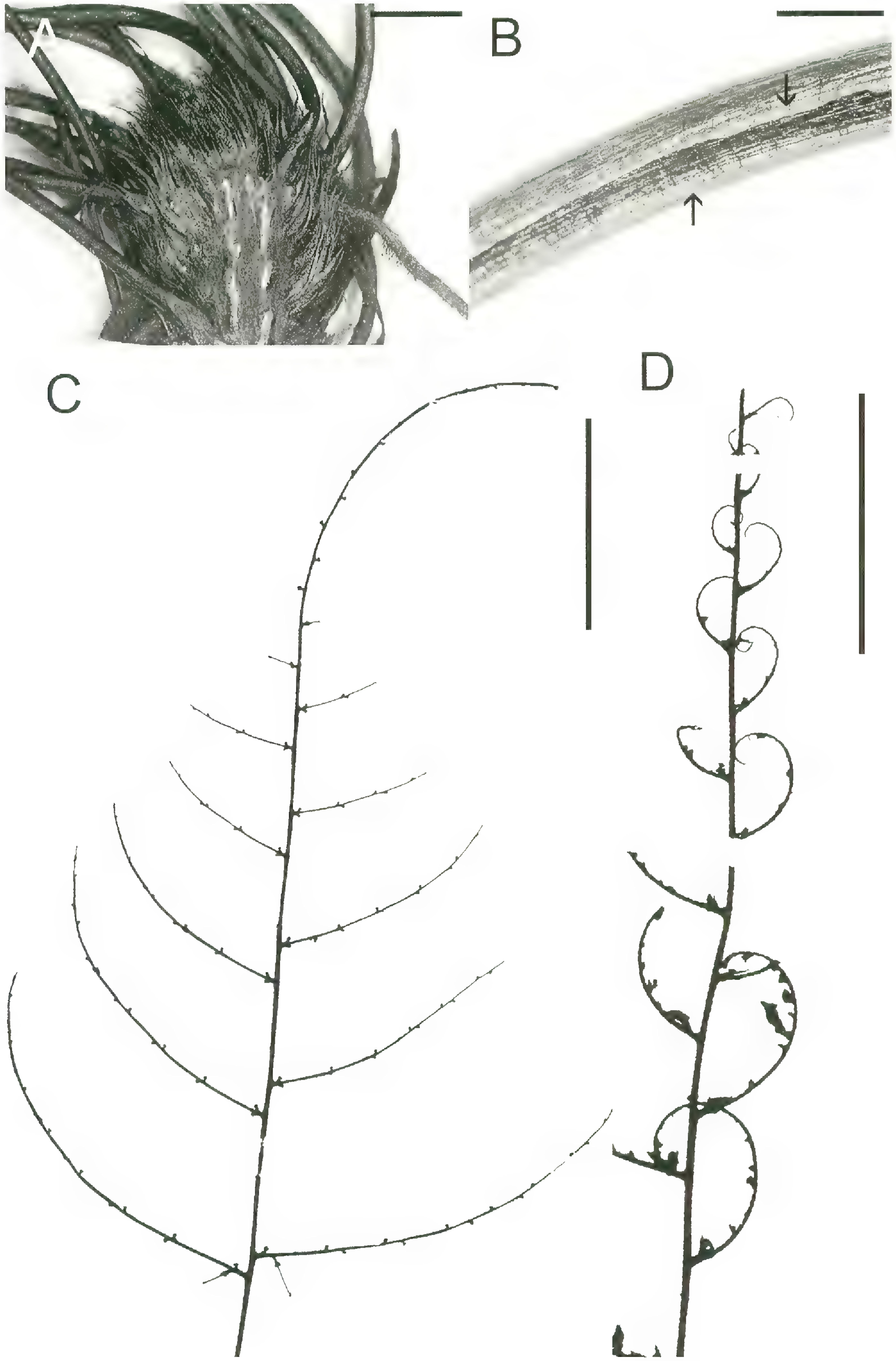

Figure 1. —A. Longitudinal section of *Adiantopsis paupercula* rhizome with bicolorous scales densely covering rhizome surface, and radially attached stipes (*C. Wright 961*, US). Scale bar = 0.25 cm. —B. Adaxial carinae (indicated by arrows) on *A. reesii* stipe (*Ekman 9987*, UC). Scale bar = 1.5 mm. —C. Persistent costae of *A. paupercula* (*H. A. Hespenheide 1191*, US) retaining their original position. —D. Marcescent costae of *A. vincentii* (*C. V. Morton 10389*, US) curling upon themselves. Scale bars C, D = 2.0 cm.

and Tryon (1982) used the carinae to distinguish *Adiantopsis* from *Cheilanthes*. However, characterization of *Cheilanthes* as lacking carinae is not accurate. Some *Cheilanthes*, such as *C. aemula* Maxon, *C. microphylla* (Sw.) Sw., and *C. wrightii* Hook. are adaxially bicarinate (Barker, pers. observ.). In the bicarinate *Cheilanthes*, the carinae are usually green or pale green, approaching the color of the laminar tissue, whereas *Adiantopsis* carinae are distinctly golden, independent of laminar color. Furthermore, carinae in *Cheilanthes* are typically restricted to the costae and costules, whereas in *Adiantopsis* they generally occur on all axes. Additionally, *Cheilanthes* carinae are contiguous with the laminar tissue. In *Adiantopsis*, with the exception of lamina and pinnae apices, carinae remain distinct from the laminar tissue. However, this may be more an architectural phenomenon than a reflection of the absence of homology. Thus, carinae distinguish *Adiantopsis* from *Cheilanthes* by their form, not their presence.

Of all axis characters, those associated with the stipes are the most taxonomically informative. In *Adiantopsis*, the stipes may grow to 47.0 cm long and 2.6 mm in diameter. Pneumatothodes were observed on stipes of all species. Taxonomic differences emerge when comparing the ratio of stipe length to overall frond length. In the pinnate Caribbean taxa, stipes are one third the overall frond length, whereas they are equal to or longer than the lamina in the pedate taxa. Stipes of *A. radiata* are consistently longer than the lamina, and in *A. paupercula* they approach equity with laminar length, being variously shorter or longer than the lamina. There are also taxonomic differences in the extent of carinae development. In *A. paupercula*, the carinae begin in the upper half of the stipe, frequently starting at the stipe mid-point. Carinae begin in the upper third and quarter of stipes in *A. pentagona* M. S. Barker & Hickey and *A. rupicola* Maxon. In *A. parvisegmenta, A. pedata* (Hook.) T. Moore, *A. reesii* (Jenm.) C. Chr., and *A. vincentii* M. S. Barker & Hickey, carinae begin at the stipe bases or in the basal half of stipes. *Adiantopsis radiata* frequently lacks carinae on the stipes, but when present, they begin at the base of the stipe. Carinae are always absent on the stipes of *A. asplenioides*.

Laminar axes in *Adiantopsis* are generally persistent. In most taxa, the original laminar axis position and form are retained even after the loss of ultimate divisions (Figure 1C). However, in senescent fronds of *A. rupicola* and *A. vincentii* the costae are marcescent and curl upon themselves becoming almost circinate in appearance (Figure 1D).

In his revision of *Lindsaea* Dryand. ex Sm., Kramer (1957: 123) noted that "In few fern genera such a great diversity of leaf-pattern is found as in *Lindsaea*." If the above statement is true for *Lindsaea*, then *Adiantopsis* may have the largest diversity of laminar variation seen in any fern genus, and it is certainly the most diverse among the cheilanthoid genera. Three basic laminar architectures occur in *Adiantopsis*; palmate, pinnate, and pedate (Figure 2). The palmate architecture is observed only in *A. radiata* (Figure 2A). In this species, the pinnae are born from a single point at the stipe apex, and no noticeable rachis is present. A pinnate laminar architecture occurs in *A. asplenioides, A. parvisegmenta, A. paupercula, A. reesii, A. rupicola*, and *A. vincentii* (Figure 2B). *Adiantopsis pedata, A. pentagona*, and *A. ×australopedata* are pedate (Figure 2C). As in pinnate species, the pinnae of pedate laminae are disposed along a central rachis. However, in the pedate taxa, the basal basiscopic pinnules of the first pinnae pair are considerably longer than the other pinnules. In the pinnate and pedate taxa, the lamina lies in the same plane as the stipe and rachis. However, in palmate *A. radiata*, the lamina is geniculate to the stipe.

The overall shape of *Adiantopsis* laminae is a reflection of architecture. Palmate *Adiantopsis radiata* has an orbiculate lamina. Pinnate taxa are variously triangular to lanceolate, or linear in *A. asplenioides*. Both pedate taxa are pentagonal, as reflected in the name of *A. pentagona*. Laminar apices in the pinnate and pedate taxa are difform, with the exception of *A. paupercula*, which is conform.

The laminae in *Adiantopsis* range from small and simple to large and complex. *Adiantopsis asplenioides* has the smallest laminae, with a maximum length of 14.5 cm and a width of 1.1 cm. It is also the simplest, with pinnate-pinnatifid to bipinnate laminae. Of the Caribbean taxa, *A. reesii* has the longest laminae at 60.0 cm, whereas the widest laminae are in *A. pentagona* at 48.2 cm wide. *Adiantopsis parvisegmenta* and *A. paupercula* may have quadripinnate laminae and are the most compound among Caribbean *Adiantopsis* taxa. However, in South America, laminae may be pentapinnate as in *A. chlorophylla*. With the exception of *A. asplenioides*, most Caribbean *Adiantopsis* laminae are 20–40 cm long and 10–20 cm wide.

Adiantopsis laminar tissues vary from papyraceous to spongiose. Papyraceous laminar tissues are found in *A. reesii* and *A. vincentii. Adiantopsis asplenioides* and *A. pedata* are chartaceous. *Adiantopsis rupicola* may have chartaceous to thin-spongiose tissue, whereas *A. radiata* and *A. pentagona* have thin-spongiose tissue. Finally, spongiose laminar tissue is found in *A. parvisegmenta* and *A. paupercula*.

Randomly dispersed on the adaxial laminar surface are white epidermal cells. These cells are hard, and probably calcified. Hydathodes are also located on the

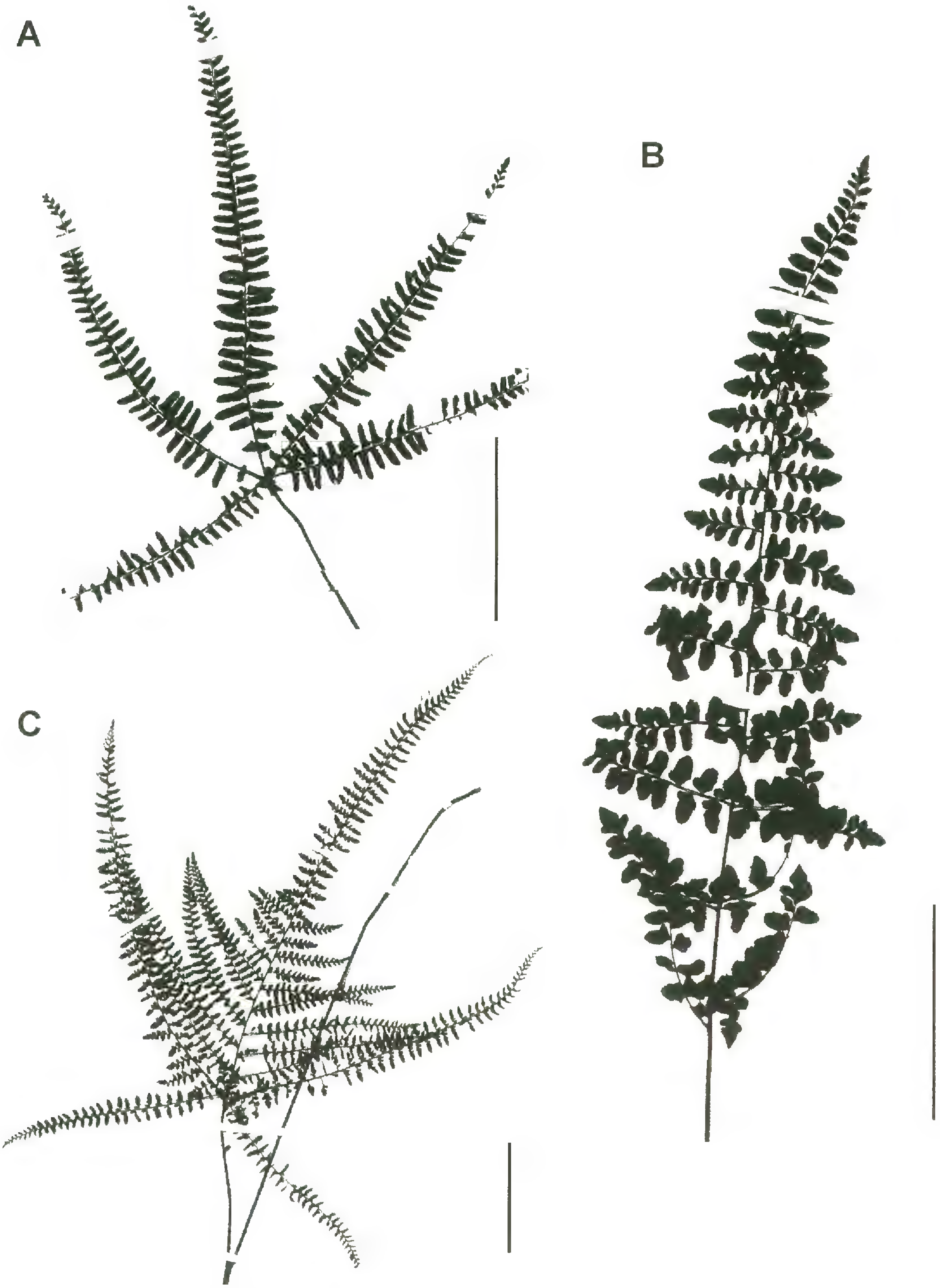

Figure 2. —A. Radiate lamina morphology of *Adiantopsis radiata* (*J. L. Main s.n.*, MU). —B. Pinnate lamina morphology of *A. rupicola* (*W. Palmer 242 & J. H. Riley*, US). —C. Pedate lamina morphology of *A. pentagona* (*C. Wright 3949*, MO). Scale bars = 5 cm.

Table 1. Sample sizes, means, standard deviations, and ranges (min, max) for Caribbean *Adiantopsis* guard cell lengths. Taxa that do not share letters are significantly different from each other ($P < 0.0001$).

Taxon	Sample size	Mean (μm)	Standard deviation (μm)	Min (μm)	Max (μm)
A. asplenioides[a]	50	52.42	3.78	45.64	57.05
A. parvisegmenta[a]	125	45.5	4.44	32.6	58.68
A. paupercula[b]	125	61.22	5.59	48.9	68.46
A. pedata[c]	125	65.86	5.88	53.79	78.24
A. pentagona[c]	125	67.04	8.85	32.6	83.13
A. radiata[a]	125	49.77	4.95	35.86	63.57
A. reesii[a]	125	44.34	4.49	32.6	53.79
A. rupicola[a]	125	49.75	4.32	42.38	57.05
A. vincentii[a]	50	45.84	3.53	40.75	53.79

adaxial surface of the laminar tissue. In *Adiantopsis*, these hydathodes are sub-marginal on single vein tips, and are generally covered with a hard, amorphous, white mass. As *Adiantopsis* prefers calcareous substrates, this material appears to be a guttation byproduct. This material, and the wall constituents of the white epidermal cells, is most likely calcium or some other mineral collected from the substrate.

Guard cells are located only on the abaxial side of the laminar tissue and are anomocytic. They may be surrounded by two, three, four, or as many as five subsidiary cells, even on the same ultimate division. Length differences do exist among the guard cells of different taxa (Table 1). The guard cells of *A. asplenioides*, *A. parvisegmenta*, *A. radiata*, *A. reesii*, *A. rupicola*, and *A. vincentii* form a group of taxa with guard cell length means centering around 45 μm. *Adiantopsis paupercula* has a mean guard cell length of 61.22 μm, whereas *A. pedata* and *A. pentagona* form a group of taxa with a combined mean guard cell length of 66.45 μm. The guard cell lengths of all three groups are significantly different from each other ($P < 0.0001$) in Tukey-Kramer pairwise comparisons.

Pinnae in *Adiantopsis* are generally triangular to fusiform. The triangular basal pinnae of the pedate taxa are strongly inequilateral, a function of the much extended basal basiscopic pinnules. All other pinnae of the pedate taxa are more or less equilateral. In *A. parvisegmenta* and *A. paupercula*, pinnae are also somewhat inequilateral with basiscopic pinnules slightly longer than the acroscopic pinnules (Figure 1C). Pinnae of *A. asplenioides* reach 6.1 mm long and 6.0 mm wide. Those of other species range to 24.1 cm long and to 19.9 cm wide. Pinnae are alternate, with the exception of the subopposite basal pinnae of the pedate taxa. In *A. radiata*, the pinnae radiate from the stipe apex. Pinnae in *Adiantopsis* are generally ascending, but a number of taxa also have patent pinnae. In *A. parvisegmenta*, *A. paupercula*, *A. reesii*, *A. rupicola*, and *A. vincentii* the proximal pinnae are frequently or occasionally arcuate, with only the distal pinnae straight. This is quite different from the curling observed in senescent fronds of *A. rupicola* and *A. vincentii* (Figure 1D). In these taxa, the incurved pinnae increase their curvature dramatically becoming circinate in appearance. In all other taxa, the senescent pinna axes retain their shape, whether straight or somewhat incurved.

Adiantopsis venation and architecture is anadromous. Pinnules are typically narrowly triangular to linear, and occasionally lanceolate. In the pinnate taxa, the basiscopic pinnules are slightly longer than the acroscopic pinnules and may be up to 7.5 cm long and 2.5 cm wide. The basal basiscopic pinnules of the pedate taxa are much longer and reach 15.3 cm in length. Pinnules may be patent to ascending.

Adiantopsis ultimate divisions are an important source of taxonomic information. For example, the ultimate divisions of *A. paupercula* are strongly articulate, with a clear enlargement and differentiation of the axis at its juncture with the laminar tissue (Figure 3A). The ultimate divisions of other *Adiantopsis* taxa, while articulate with age, lack the swollen and distinct articulation point of *A. paupercula* (Figure 3B). The ultimate divisions of *A. parvisegmenta* are by far the smallest of the Caribbean taxa, reaching a maximum size of 3.5 mm long by 2.5 mm wide. The ultimate divisions of other *Adiantopsis* taxa generally overlap in size, with a maximum length of 13.5 mm in *A. radiata* and maximum width of 4.5 mm in *A. paupercula*. There is considerable overlap in ultimate division shapes among Caribbean *Adiantopsis*, with shapes ranging from oblong, to oblanceolate, lanceolate, elliptic, trullate, and rhombic. Ultimate division bases are generally cuneate and are often uniauriculate on the acroscopic side. The apices of *A. reesii* and *A. pedata* ultimate divisions are acute and distinctly toothed, whereas in other taxa they are generally acute to round and entire. *Adiantopsis asplenioides* ultimate divisions are distinctly lobed, whereas the margins of other taxa are entire to crenulate (Figure 3C, D, E). All ultimate divisions are

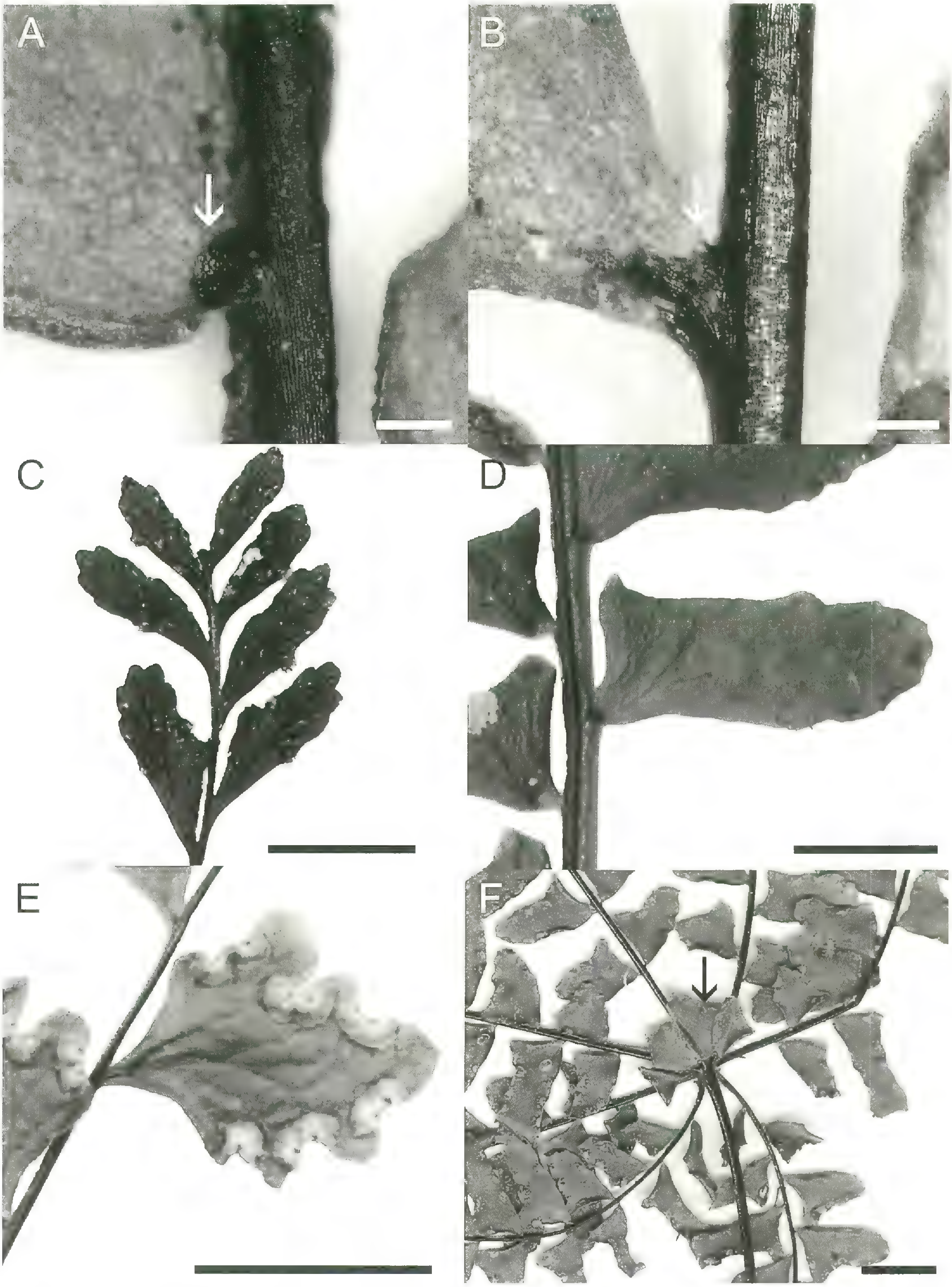

Figure 3. —A. Swollen stalk apex at junction with lamina tissue (arrow) of *Adiantopsis paupercula* (*C. Wright 962*, UC). Ultimate divisions are articulate and break cleanly at this swollen point. Scale bar = 1 mm. —B. Non-swollen stalk apex at junction with lamina tissue (arrow) of *A. pentagona* (*J. G. Jack 7903*, US). Ultimate divisions are articulate, but do not break cleanly from the stalk. Scale bar = 0.3 mm. —C. Toothed ultimate division apices of *A. reesii* (*E. L. Ekman 10608*, US). —D. Round, entire ultimate division apices of *A. radiata* (*J. A. Shafer 3777*, F). —E. Lobed ultimate divisions of *A. asplenioides* (*Bro. Alain 1226 & Acuna*, US). —F. Abaxial view of basal flabellate divisions of *A. radiata* (*G. L. Webster 13425*, MICH), indicated by arrow. The divisions are attached to the stipe apex between pinna pairs. Note similarity of shape between basal ultimate and flabellate divisions. Sori are visible on these basal flabellate divisions, which suggests they are homologous to ultimate divisions of the pinnae. Scale bars C–F = 0.5 cm.

deciduous with persistent stalks ranging from 0.1–6.3 mm in length.

Adiantopsis radiata possesses basal flabellate divisions, an autapomorphy for this taxon. As their name implies, these divisions are generally flabellate and occur on the stipe apex between pinnae (Figure 3F). These basal flabellate divisions appear to be homologous to ultimate divisions. The overall shape of basal pinnules and these flabellate divisions is similar (Figure 3F). Additionally, the basal flabellate divisions become fertile with the other ultimate divisions. They are likely a by-product of axial compression in *A. radiata*, as they appear to be ultimate divisions developed within the stipe crown at a point below the stipe surface. These basal flabellate divisions are usually restricted to mature *A. radiata* plants with larger than average fronds and more than five pinnae.

Adiantopsis indument consists of hairs and scales. The hairs are septate-capitate, with well defined septa and bulbous apical cells. On the axes, they are concentrated at axis junctions and distributed diffusely across the abaxial surface. They are generally appressed and may be up to ten cells long, although most are much shorter. Septate-capitate hairs are also found on the abaxial laminar tissue. Typically, the laminar hairs are three celled, although rarely may they be two or four celled. These septate-capitate hairs are clavate, with an elongate basal cell, a relatively short middle cell, and a bulbous apical cell. In some taxa, such as *A. parvisegmenta*, the apical cell is very bulbous and overarches the middle cell. In *A. pentagona* and others, the apical cell, while still bulbous, is generally elongate and does not overlap the middle cell. The basal cells are usually clear, but the middle and apical cells are variable, being red, gold, white, or clear, but usually the two are not the same color. While some taxonomic trends in color have been observed, they are too variable to reliably differentiate taxa. These septate-capitate hairs are present in some putative South American *Adiantopsis* taxa as well and apparently demonstrate some taxonomic utility (Ponce & Morbelli, 1989). Their ultimate taxonomic use within the genus can be re-evaluated once all *Adiantopsis* taxa have been fully examined.

The type of hairs observed in *Adiantopsis* appears to be a synapomorphy for the genus. Tryon and Tryon (1982) stated that *Adiantopsis* is closely related to the *Cheilanthes microphylla* group of *Cheilanthes*. However, a number of differences between the hairs of the two groups are observed. Hairs of the *C. microphylla* group are much longer, more filamentous, and with indistinct or oblique cross walls, characteristics not associated with *Adiantopsis*. In the *C. microphylla* group, both adaxial and abaxial surfaces of the lamina and axes are covered with hairs, whereas in *Adiantopsis* the hairs are restricted to abaxial surfaces. Additionally, hairs in the *Cheilanthes* taxa are much denser than *Adiantopsis* hairs. The septate-capitate hairs of *Adiantopsis* have not yet been observed in *Cheilanthes*.

Adiantopsis scales are found on the rhizome, stipe, and laminar axes. Rhizome scales are bicolorous (Figure 1A), with persistent, black to dark brown centers and deciduous, golden or, in *A. asplenioides*, white, translucent margins. Scales densely cover the rhizome surface. These scales are generally lanceate to acicular, with truncate bases, entire to slightly repand margins, and acute, gland tipped apices. The rhizome scales of all species are similar and generally lack taxonomic value.

Stipe scales are uniformly concolorous and tan. Overall, the scales range from lanceolate to acicular, or occasionally subulate. *Adiantopsis* stipe scales are frequently biauriculate and appear pseudopeltate, but some scale bases are not auriculate and are truncate. Scale margins range from entire to slightly repand. Apices are acute to attenuate and gland tipped. In all taxa, stipe scales are deciduous, as the remnants of scale bases are often observed and the number of scales varies considerably. These scale characters possess relatively little taxonomic value. However, the stipe scales of *A. parvisegmenta*, *A. paupercula*, *A. reesii*, *A. rupicola*, and *A. vincentii* are divergent from the stipe surface, whereas *A. pedata*, *A. pentagona*, and *A. radiata* stipe scales are appressed to the stipe surface, only occasionally divergent. Stipe scales are distributed at the base of stipes, typically to a maximum of 7.1 cm above the rhizome. However, stipe scales on some *A. reesii* specimens are distributed along the entire length of the stipe to the rachis. It is possible that stipe scales are distributed higher on the stipes of other taxa and are simply not observed because of their deciduous nature. Stipe scales are conspicuously absent in *A. asplenioides*.

Distal to the stipe, scales are rarer, more easily overlooked, and are usually no more than five cells wide and eight cells long. They are concentrated at laminar axis junctions and are diffusely scattered on abaxial axis surfaces. Scales are typically lanceate in overall shape and are gland tipped. Some scales are biseriate and closely resemble axis hairs, suggesting that hairs and scales in *Adiantopsis* form a developmental and evolutionary continuum. Laminar scales are not taxonomically informative.

Venation in *Adiantopsis* is free. In most species, veins are pseudodichotomous and anadromous, although in *A. paupercula* veins are flabellate. Veins are typically obscure to occult and are generally im-

mersed in the laminae. Veins always terminate marginally or sub-marginally in adaxial hydathodes.

Adiantopsis sori are marginal and consistently uninerved. Sori occur on both acroscopic and basiscopic division margins; in *A. asplenioides* they frequently occur on the interior sides of lobes. For the most part, a single, distinct pseudoindusium covers each sorus, although in *A. asplenioides*, pseudoindusia may be partially confluent across sinus bases. The generally distinct pseudoindusia distinguish *Adiantopsis* from *Cheilanthes*, in which a series of confluent pseudoindusia comprise the entire margin of an ultimate division (Tryon & Tryon, 1982). *Adiantopsis* pseudoindusia are typically lunate to quadrangular, with entire to erose margins.

Sporangia in *Adiantopsis* show a mixed development and are generally subglobose and long stalked. The stalks are typically three cells long. However, in *A. asplenioides*, and an undescribed Bolivian and Paraguayan taxon, the sporangia are globose and essentially sessile, with apparently only a single cell layer between the sporangium and receptacle. The number of indurated arcus cells shows taxonomically informative trends in *Adiantopsis*. Indurated arcus cell numbers show narrow ranges of variation, with modes that are useful for discriminating among taxa (Figure 4). For example, *A. pedata*, *A. reesii*, and *A. vincentii* have a mode of 14, *A. parvisegmenta*, *A. paupercula*, *A. pentagona*, and *A. rupicola* have a mode of 16, *A. asplenioides* has a mode of 11, and *A. radiata* has a mode of 20. *Adiantopsis* sporangia generally contain 64 spores; however *A. asplenioides* has 32 spores per sporangium.

Indurated arcus cell sizes also differentiate taxa into two groups (Table 2). One group consists of the pedate taxa, with a mean indurated arcus cell height of approximately 48 μm. All other taxa are included in the second group, with a mean indurated arcus cell height of approximately 38 μm. These two groups were significantly different from each other in Tukey-Kramer pairwise comparisons.

Adiantopsis spores are tetrahedral-globose and generally echinate (Figure 5). The only species to deviate from this is *A. asplenioides*, which has cristate spores with anastomosing strands below the muri (Figure 5B). Among the echinate spored species, some notable differences are observed. The echinae bases of *A. pedata*, *A. pentagona*, and *A. radiata* are all dissected, whereas the echinae bases in other taxa are complete. Also, the echinae of *A. paupercula* spores are more compact relative to the echinae of other species' spores. The laesurae are obscured by the ornamentation in all spores except *A. asplenioides*; its laesurae are easily observed with a dissecting microscope. Spore sizes in *Adiantopsis* are divided into three distinct groups all statistically different from each other, as determined by Tukey-Kramer pairwise comparisons (Table 3). The first group, with spore lengths averaging around 37 μm, includes *A. parvisegmenta*, *A. paupercula*, *A. radiata*, *A. reesii*, *A. rupicola*, and *A. vincentii*; *Adiantopsis pedata* and *A. pentagona* compose the second group with average spore lengths of approximately 46 μm. Finally, *A. asplenioides* forms a third group, with a mean spore length of 75.83 μm.

The echinate spores of *Adiantopsis* help distinguish it from *Cheilanthes*. The spore ornamentation of *Cheilanthes* is variable, with only a few Australian species possessing echinate spores (Tryon & Tryon, 1982). Even in light of these echinate Australian *Cheilanthes*, Tryon and Tryon (1982) recognized *Adiantopsis* based primarily on the echinate spore ornamentation, as the echinate Australian *Cheilanthes* are easily distinguished from *Adiantopsis* by vegetative characters. The only exception to echinate spores in Caribbean *Adiantopsis* is *A. asplenioides*. Given its other unique characters, *A. asplenioides* may belong in another, perhaps new, genus, although some putative South American *Adiantopsis* taxa that are currently placed in *Cheilanthes* also have cristate spores (Ponce & Morbelli, 1989). *Adiantopsis asplenioides* is retained here only until a full analysis of South American *Adiantopsis* is completed. If *A. asplenioides* is segregated from *Adiantopsis*, echinate spores would characterize the genus.

Taxonomic History

In 1852, Fée erected the genus *Adiantopsis* for various species in *Adiantum* L., *Cheilanthes*, and *Hypolepis* Bernh. with distinct pseudoindusia for each sorus. Originally, Fée included four species in *Adiantopsis*: *A. capensis* (Sw.) Fée, *A. chlorophylla*, *A. paupercula*, and *A. radiata*. He designated *A. paupercula* as the type species for the genus. Christensen (1906) later lectotypified the genus with *A. radiata*; this was unnecessary because Fée (1852: 145) clearly designated (with the term *Diagnosis*) *A. paupercula* by referencing Kunze's (1850) publication of the species. As a result, some authors (e.g., Mickel & Smith, 2004) recognize *A. radiata* as the type, whereas others (e.g., Tryon & Tryon, 1982; Proctor, 1985) recognize *A. paupercula*. It seems clear to us that *A. paupercula* should be recognized as the type species for the genus, as Fée unambiguously designated it as such.

Fée (1857) also published two subgenera within *Adiantopsis*: *Euadiantopsis* Fée (= *Adiantopsis*) and *Cheilanthastrum* Fée. Although he did not provide characters for the subgenera, an evaluation of the list

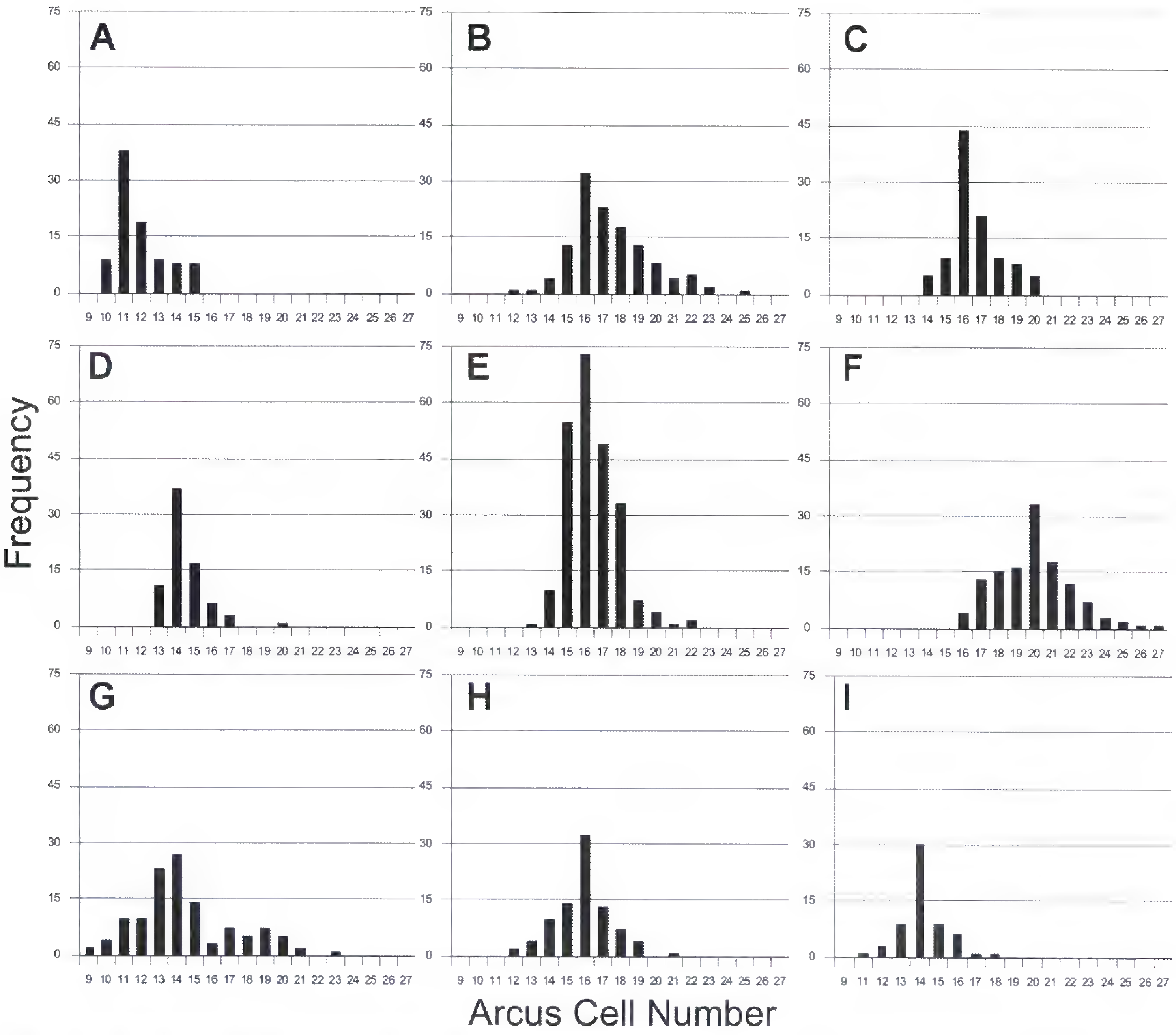

Figure 4. Frequency histograms of *Adiantopsis* arcus cell number. X-axis is arcus cell number, Y-axis is frequency (absolute value). —A. *A. asplenioides.* —B. *A. parvisegmenta.* —C. *A. paupercula.* —D. *A. pedata.* —E. *A. pentagona.* —F. *A. radiata.* —G. *A. reesii.* —H. *A. rupicola.* —I. *A. vincentii.*

Table 2. Sample sizes, means, standard deviations, and ranges (min, max) for Caribbean *Adiantopsis* areus cell height. Taxa that do not share letters are significantly different from each other ($P < 0.0001$).

Taxon	Sample size	Mean (μm)	Standard deviation (μm)	Min (μm)	Max (μm)
A. asplenioides[a]	50	34.38	2.47	30.97	39.12
A. parvisegmenta[a]	125	40.78	3.19	32.6	48.9
A. paupercula[a]	125	40.59	3.3	35.86	47.27
A. pedata[b]	125	48.8	3.55	40.75	55.42
A. pentagona[b]	125	48.66	4.46	40.75	58.68
A. radiata[a]	125	39.04	2.76	30.97	46.46
A. reesii[a]	125	36.34	6.47	21.19	48.9
A. rupicola[a]	125	37.16	3.33	32.6	42.38
A. vincentii[a]	50	38.01	4.31	32.6	52.16

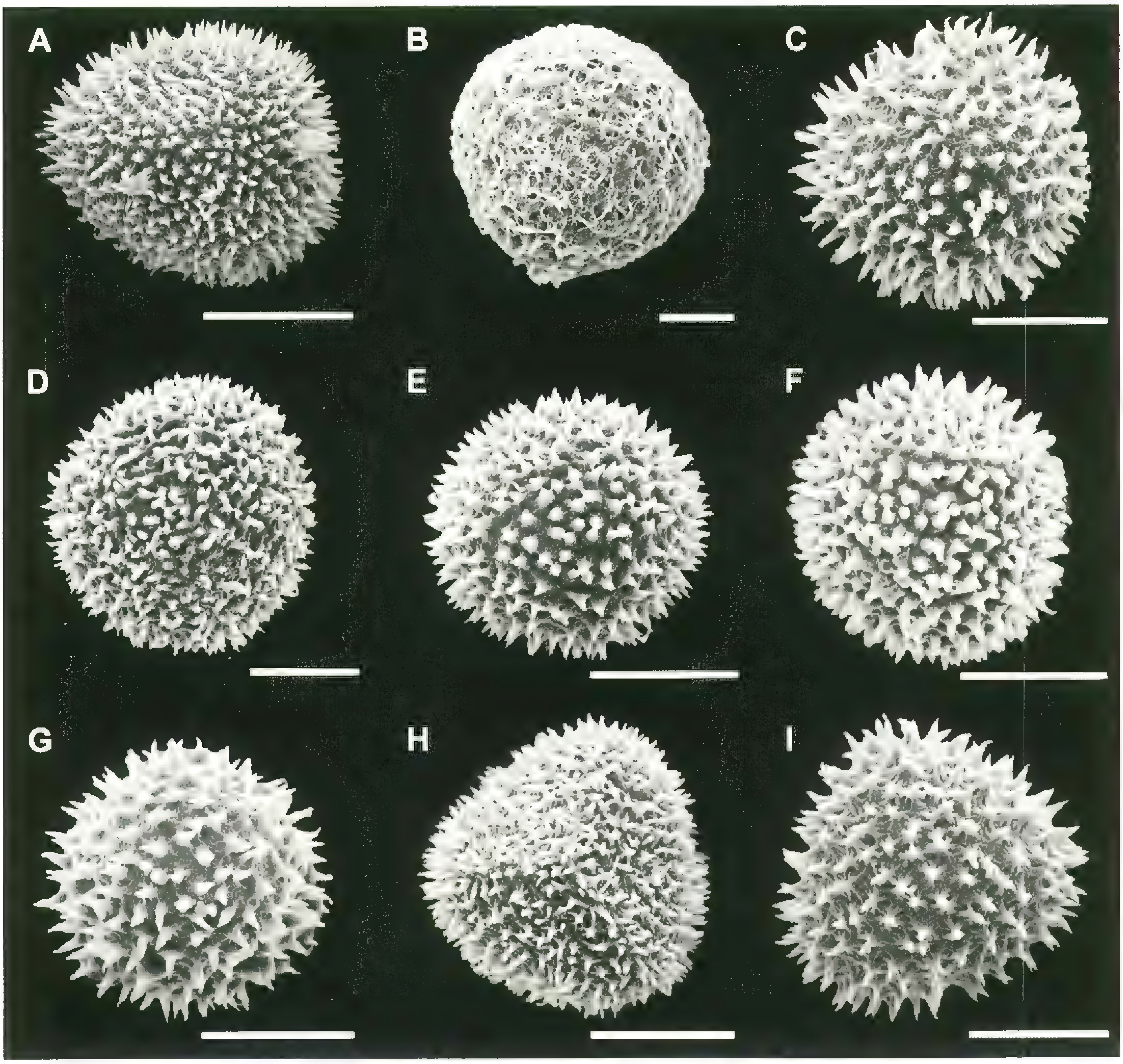

Figure 5. Electron micrographs of Caribbean *Adiantopsis* spores. —A. Echinate *A. radiata* spore with dissected echinae bases (*J. A. Shafer 3777*, F). —B. Cristate *A. asplenioides* spore with anastomosing strands beneath the muri (*Br. Main A1226*, US). —C. Echinate *A. parvisegmenta* spore with complete echinae bases (*J. G. Jack 6877*, US). —D. Echinate *A. paupercula* spore with compact echinae (*Maxon 1239*, US). —E. Echinate *A. reesii* spore with complete echinae bases (*E. L. Ekman 9987*, F). —F. Echinate *A. rupicola* spore with complete echinae bases (*Britton et al. 3497*, US). —G. Echinate *A. vincentii* spore with complete echinae bases (*Egger 5399*, F). —H. Echinate *A. pedata* spore with dissected echinae bases (*Harris 10878*, US). —I. Echinate *A. pentagona* spore with dissected echinae bases (*C. Wright 3949*, US). Scale bars = 20 μm.

Table 3. Sample sizes, means, standard deviations, and ranges (min, max) of Caribbean *Adiantopsis* spore lengths. Taxa that do not share letters are significantly different from each other ($P < 0.0001$).

Taxon	Sample size	Mean (μm)	Standard deviation (μm)	Min (μm)	Max (μm)
A. asplenioides[a]	50	75.83	6.74	58.68	88.02
A. parvisegmenta[a]	125	40.59	2.41	34.23	47.27
A. paupercula[b]	125	41.4	2.96	35.86	45.64
A. pedata[c]	125	45.5	3.85	38.31	54.61
A. pentagona[c]	125	45.77	3.4	40.75	58.9
A. radiata[b]	125	39.94	2.35	34.23	47.27
A. reesii[b]	125	36.34	2.44	30.97	44.83
A. rupicola[b]	125	37.75	1.68	34.23	40.75
A. vincentii[b]	50	38.16	3.67	32.6	44.01

of species he included in each subgenus identified possible distinguishing characters. Subgenus *Euadiantopsis* (*Adiantopsis radiata*, *A. paupercula*, and *A. pteridoides* Moore [= *Cheilanthes pteridoides* Sw.]) is apparently characterized by more oblong ultimate divisions, whereas those of subgenus *Cheilanthastrum* (*Adiantopsis chlorophylla*, *A. spectabilis* [= *A. chlorophylla*], and *A. capensis* [= *Cheilanthes capensis*]) are more elliptic to oblanceolate. Additionally, two of the taxa in subgenus *Euadiantopsis*, *A. paupercula* and *A. radiata*, have ultimate division shapes that are more like those found in *Adiantum* than in *Cheilanthes*, whereas the species placed in subgenus *Cheilanthastrum* have ultimate division shapes more similar to *Cheilanthes*. Although these subgenera are not recognized here, they do reflect morphological trends that have caused taxonomic confusion in the past.

Past authors have not always recognized *Adiantopsis*. For example, Hooker and Baker (1883) placed *Adiantopsis* as a subgenus within *Cheilanthes* in their *Synopsis Filicum*. However, they did use Fée's (1852) characters to recognize subgenus *Adiantopsis*. The placement of *Adiantopsis* within *Cheilanthes* is in line with their overall generic concept, which recognized a small number of large fern genera with a substantial number of subgenera. Copeland (1947) also did not recognize *Adiantopsis*, suggesting that it was insufficiently distinct to warrant generic status; he placed it in synonymy under *Cheilanthes*.

Other authors have recognized *Adiantopsis*, but with qualification. For example, Smith (1981) suggested that if species such as *A. chlorophylla* and *A. seemannii* (Hook.) Maxon are included in *Adiantopsis*, the distinction between it and *Cheilanthes* disappears. Specifically, he cited the morphological similarities of these species to *C. aemula* and *C. microphylla*.

Many other researchers have recognized *Adiantopsis* as construed by Fée. Christensen (1906) recognized it in his *Index Filicum*. Maxon (1908) also recognized *Adiantopsis* and published a useful synopsis of the Cuban taxa. Most modern tropical fern floras recognize *Adiantopsis* as distinct from *Cheilanthes* (Sehnem, 1959, 1961, 1972; Tryon & Tryon, 1982; Proctor, 1985; Lellinger, 1989; Proctor, 1989; Tryon et al., 1990; Pacheco, 1995; Mickel & Smith, 2004). In general, these researchers, and Fée, utilized a more narrowly defined generic concept than either Hooker and Baker (1883) or Copeland (1947). Only Copeland (1947) articulated problems with the recognition of *Adiantopsis*, although he did not refer to a number of distinctive characters, such as spore ornamentation, adaxial carinae, and hair morphology.

Although *Adiantopsis* has been included in many fern floras and indices, little comprehensive research has been done at the species level. One of the most significant contributors to species level taxonomy in *Adiantopsis* was Sehnem. He published a series (1959, 1961, 1972) of keys and species descriptions for various floras in southeastern Brazil and the tri-border region of Argentina, Brazil, and Paraguay. In these treatments, he provided excellent keys to the species of the region using characters that were overlooked by other pteridologists. Further, he provided some clarification to the *A. chlorophylla* species complex by recognizing two new species, *A. perfasciculata* and *A. occulta*. Unfortunately, most pteridologists, including Tryon and Tryon (1982), were unaware of Sehnem's *Adiantopsis* research.

Tryon and Tryon (1982) were the most recent taxonomists to review *Adiantopsis*. They regarded the genus as closely related to their *Cheilanthes microphylla* group (their *Cheilanthes* group 1). That group and *Adiantopsis* share dark axes and less hair than other cheilanthoid groups. The main character used by Tryon and Tryon (1982) to distinguish *Adiantopsis* from *Cheilanthes* was the echinate spores in *Adiantopsis*. Additionally, they noted adaxially bicarinate laminar axes, asymmetrical and articulate ultimate divisions, and distinct indusia covering single sori as distinguishing features of *Adiantopsis* (Tryon & Tryon, 1982).

Tryon and Tryon (1982) recognized seven *Adiantopsis* species in total, including *Adiantopsis paupercula, A. pedata, A. radiata,* and *A. reesii* from the Caribbean. In their treatment, they sank *A. rupicola* into *A. reesii*, stating that it does not appear to be distinct, and considered *A. asplenioides* to be a juvenile form of *A. paupercula*. With regard to South American taxa, Tryon and Tryon (1982) did recognize one of Sehnem's species, *A. minutula*, but did not acknowledge his *A. perfasciculata* and *A. occulta*. It is not clear why they did not recognize these two distinctive species. Although Tryon and Tryon's (1982) treatment of *Adiantopsis* failed to mention some key species, they provided the most comprehensive overview of the genus ever published.

Recent molecular work by Gastony (unpublished data) supports the generic status of *Adiantopsis*. A molecular analysis with *rbc*L DNA sequences supports a sister relationship between *A. radiata* and the South American *A. chlorophylla* with 23 synapomorphies and 100% bootstrap support (Gastony, unpublished data). The analysis included representatives of cheilanthoid genera from all geographic regions and provides support that *Adiantopsis* is a distinct genus. Further, it refutes Smith's (1981) contention that including *A. chlorophylla* in *Adiantopsis* makes the genus indistinguishable from *Cheilanthes* because of morphological similarity to *C. aemula*. *Cheilanthes aemula* was included in Gastony's (unpublished data) analysis and was distantly related to the *Adiantopsis* group. Thus, it appears that any morphological similarity observed by Smith (1981) between the two taxa is likely convergent. Additional molecular research with a broader sampling of *Adiantopsis* is needed to evaluate the boundaries of the genus, but it does appear to be phylogenetically distinct from other *Cheilanthes*.

Species Concept

In this revision of *Adiantopsis*, a morphological species concept was employed to discriminate species. Essentially, if groups of collections were morphologically distinct they were recognized as distinct taxa; if not, they were maintained as a single species. Implicit in this usage of the morphological species concept is the assumption that morphological distinctness reflects underlying genetic distinctness produced as a result of unique evolutionary histories for each species. If future research using molecular data, such as population genetic markers that sample multiple loci across the genome, does not identify partitioned genetic variation, then species boundaries should be re-evaluated.

Evolutionary Relationships

Based on a comparison of morphological data obtained from Caribbean collections, a total of nine morphological species are recognized for this region. Of these nine species, seven are putative diploids and two are putative polyploids. In *Adiantopsis*, chromosome counts are known only from *A. radiata*. The counts of $n = 30$ (Walker, 1973; Smith & Foster, 1984) represent the base number for the cheilanthoid genera, and thus it is assumed that *A. radiata* is a diploid species. As material was not available to count the chromosomes of other *Adiantopsis* taxa, indirect estimates of ploidy level were used. Barrington et al. (1986) demonstrated that guard cell and spore lengths in leptosporangiate ferns frequently correspond to ploidy level. Indurated arcus cell size has also been correlated with ploidy level by Butters and Tryon (1948). Using these cell sizes and spore length (Tables 1, 2, 3), the ploidy levels of *Adiantopsis* taxa were estimated, with *A. radiata* serving as a reference for the diploid ploidy level. These data partition the nine species into two statistically significant groups. All pinnate taxa and *A. radiata* form a group of putative diploid species, whereas the two pedate taxa appear to be polyploid species, most likely tetraploids. The pedate taxa consistently possess larger cell sizes. The cell length differences between putative diploid and tetraploid *Adiantopsis* taxa are comparable to differences observed between diploid and tetraploid leptosporangiate ferns by Barrington et al. (1986) and Butters and Tryon (1948). Based on these data, *A. pedata* and *A. pentagona* are supported as tetraploid species, whereas all other Caribbean taxa appear to be diploid.

Two exceptions to this pattern in cell size exist. Guard cells of *Adiantopsis paupercula* are somewhat larger than all other putative diploid taxa, but not quite as large as those of the putative tetraploid taxa (Table 1). Spore and indurated arcus cell size place this species with the putative diploid taxa (Tables 2, 3). Its not clear why its guard cells show this intermediacy. Given that its spore and indurated arcus cell sizes are within the putative diploid range, it seems probable that this is a diploid taxon and that its guard cell lengths are influenced by other, unknown factors.

The other exception is *Adiantopsis asplenioides*, a species with a number of unique characteristics among Caribbean *Adiantopsis*. Guard cell and indurated arcus cell sizes group this taxon with other putative diploids (Tables 1, 2). However, it has the largest spore size of all *Adiantopsis* taxa (Table 3), it is the only species with 32 spores per sporangium, and it

has indurated pseudoindusia that completely and persistently cover the sori. Two hypotheses may explain these anomalous features. First, the species may be apogamous, a hypothesis supported by the reduced spore number (Evans, 1964; Klekowski, 1973). Alternatively, the spore number may be a function of a reduced number of spore mother cells and a greater resource allocation to fewer spores. Under this hypothesis, the large spores are probably not indicative of a higher ploidy level but rather are an adaptation for limiting spore dispersal. Barrington et al. (1986) observed a similar pattern in *Adiantum pedatum* ssp. *calderi* Cody, a fern that is limited to serpentine rocks. He hypothesized that the large spores may limit spore dispersal and thus prevent them from leaving the "serpentine islands" to which they are adapted. *Adiantopsis asplenioides* appears to fit Barrington et al.'s (1986) model well, as it is a serpentine species with very large spores and based on other features appears to be a diploid. Further, the persistent and indurated pseudoindusia of *A. asplenioides* may represent an additional modification to limit spore dispersal. Thus, the reduced spore number, large spores, and indurated pseudoindusia appear to represent a suite of characters adaptive in keeping propagules within its geographically restricted edaphic niche.

Adiantopsis pedata and *A. pentagona* are hypothesized to be allotetraploid derivatives between *A. radiata* and two different pinnate taxa. A hybrid origin for the pedate Caribbean taxa is supported by the occurrence and morphology of the sterile hybrid *A.* ×*australopedata* in South America. This taxon documents that the pedate laminar morphology is of hybrid origin between *A. radiata* and a pinnate second parent (Hickey et al., 2003). Also, the dissected echinae bases on spores of *A. radiata* and the pedate taxa support *A. radiata* as one parent, as all other taxa have complete echinae bases. Additional support is evidenced by common laminar development in the two pedate taxa and *A. radiata*. The fronds of young plants, as estimated by rhizome size, are strongly ternate in both species; progressively older, larger plants of these species show increasingly complex frond development. In *A. pedata* the basal basiscopic pinnules become extended and the penultimate pinna pairs enlarge, becoming increasingly prominent. In *A. radiata*, additional pinnae pairs are added to the stipe apex. This pattern of growth is only found in *A. radiata*, *A.* ×*australopedata*, and the pedate Caribbean taxa. The pinnate *Adiantopsis* taxa lack such ontogenetic architectural changes and show a common architecture on both young and old plants.

Adiantopsis reesii is supported as the second parent of *A. pedata* on the basis of crenulate apices and generally ascending ultimate divisions. Additionally, the carinae of *A. reesii* and *A. pedata* start at stipe bases or in the basal half (*A. pedata*) or quarter (*A. reesii*) of stipes. Both species also share a mode of 14 indurated arcus cells. An *A. reesii* × *A. radiata* origin for *A. pedata* is further supported by the distributions of the taxa, as collections of *A. pedata* are currently only known from areas where the three co-occur.

Numerous morphological comparisons support *Adiantopsis rupicola* as the most likely second parent of *A. pentagona*. The overall ultimate division shape of *A. pentagona* compares most favorably with the generally trullate divisions observed in *Adiantopsis rupicola*. Furthermore, the acute and generally entire ultimate division apices of *A. pentagona* reflect that character state in *A. rupicola*. The generally patent nature of *A. pentagona* ultimate divisions compares favorably with the patent disposition of the ultimate divisions in *A. rupicola*, and both *A. rupicola* and *A. pentagona* have a mode of 16 indurated arcus cells. Finally, the carinae in *A. rupicola* and *A. pentagona* start in the upper portions of stipes (upper ⅓ in *A. pentagona* and ¼ in *A. rupicola*), a character unique to these two species.

Adiantopsis pentagona, however, is quite variable, and there are suggestions that it may contain yet another cryptic species. Evidence for this comes from some *A. pentagona* specimens that have relatively small ultimate divisions, larger and slightly more compound laminae, and somewhat revolute fertile divisions. It should be noted, however, that all of these character states tend to intergrade across the suite of specimens referable to *A. pentagona*, and it is not clear from this morphological analysis whether the observed variation is due to habitat and ecological differences among plants, simple genetic variation, or multiple origins with different maternal parentages (e.g., *A. rupicola* the maternal parent for some specimens and *A. radiata* for others). Alternatively, *A. pentagona* may be a case of cryptic allotetraploids wherein two distinct species share a common *A. radiata* parent, but each has a different pinnate second parent. The variation in character morphology mentioned above could easily be accounted for if *A. parvisegmenta* was a second parent of some collections. The geographic distribution of specimens does not provide any insight about the source of the morphological variation, and resolution may require molecular analyses. Future molecular studies of this group should encompass the morphological range of *A. pentagona* specimens, *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*, because any one could be a genetic contributor.

TAXONOMY

Adiantopsis Fée, Gen. Filic. [Mém. Foug. 5] 145. 1852. TYPE: *Adiantum pauperculum* Kunze [= *Adiantopsis paupercula* (Kunze) Fée].

Rhizomes erect, ascending, decumbent, or repent, stiff; *scales* dense, overlapping, persistent, bicolorous with a black, dark brown, or atrocastaneous center and ephemeral, golden or translucent margins, acicular, lanceate, lanceolate, linear, or rarely subulate, basifixed or pseudopeltate, bases truncate or cordate, margins entire, slightly repand, or repand, apices acute, attenuate, acuminate, or cuneate, gland tipped. *Fronds* aggregated, strict or erect. *Stipes* persistent, atropurpureous, atrocastaneous, or castaneous, always, occasionally, rarely, or never bicarinate adaxially, with scattered pneumatothodes; *carinae* when present, golden; *scales* when present, deciduous, divergent or appressed, concolorous, tan, or bicolorous with broad castaneous to tan center and golden margins, acicular, lanceate, lanceolate, or rarely subulate, pseudopeltate or basifixed, bases biauriculate, truncate, or cordate, margins entire, slightly repand, or repand, apices acute or attenuate, gland tipped; *hairs* diffuse, rare, septate-capitate or rarely ciliform. *Laminae* pinnate, pedate, or palmate, drying brown, green, dull green, dark green, yellow-green, olive-green, or black, apices difform or conform, attenuate, long attenuate, acuminate, acute, or cuneate; *laminar tissue* papyraceous, chartaceous, thin-spongiose, or spongiose, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal or in sinuses surrounded by white to pale blue epidermal cells; *hairs* diffuse abaxially, septate-capitate, three celled; *stoma* abaxial, complanate or impressed, anomocytic. *Laminar axes* persistent or marcescent with costae curling acroscopically, atropurpureous, atrocastaneous, or castaneous, grading into lamina and taking its color and texture, or not grading into lamina, adaxially bicarinate; *carinae* golden or colored as axis, interrupted at axis junctions, grading into lamina or not grading into lamina; *scales* when present, concentrated at rachis-costa junctions, diffuse abaxially, deciduous, appressed or patent, concolorous, tan, linear, lanceate, narrowly lanceolate, narrowly rhombic, narrowly triangular, or biseriate, basifixed, bases truncate, acute, or cuneate, margins entire, apices acute or attenuate, gland tipped; *hairs* concentrated at axis junctions, diffuse abaxially, septate-capitate. *Pinnae* ascending, patent, or spreading radially from stipe apex, alternate, sub-opposite, or opposite, incurved in basal half of lamina and straight distally, or straight, narrowly triangular, linear, triangular, narrowly fusiform, widely rhombic, oblong, or obovate, inequilateral, slightly inequilateral, or equilateral, apices attenuate, acute, or round. *Pinnules* anadromous, slightly ascending, patent, or ascending, linear, narrowly triangular, or narrowly lanceate, apices acute, cuneate, attenuate, or obtuse. *Ultimate divisions* patent, slightly ascending, or ascending, deciduous, articulate or strongly articulate, oblong, narrowly oblong, oblanceolate, obovate, narrowly elliptic, elliptic, flabellate, trullate, lanceolate, ovate, widely rhombiform, or rhombiform, bases cuneate, acute, or truncate, may be uniauriculate acroscopically, margins entire, crenulate, slightly crenulate, or deeply lobed, apices acute, round, or acuminate; *stalks* persistent, may be swollen at junction with laminar tissue. *Veins* free, pseudodichotomous and anadromous or flabellate, immersed or impressed in lamina, occult, obscure, or prominent. *Sori* marginal on both acroscopic and basiscopic margins, uninerved. *Pseudoindusia* distinct or occasionally confluent, lunate, quadrangular, reniform, or subreniform, green to white proximally and hyaline distally, black maculate, hyaline, or white to pale blue, margins slightly erose, entire, or erose. *Sporangia* subglobose to globose, long stalked to sessile. *Spores* 64 or 32 per sporangium, tetrahedral globose, golden or white at maturity, white to pale yellow when immature, echinate or densely echinate with echinae bases complete or dissected, or cristate with anastomosing strands below the muri, laesura obscured by ornamentation or not. *Chromosome number* $2n = 60$ (Walker, 1973; Smith & Foster, 1984).

Generic distribution. The Caribbean and central Mexico to Central America, and through northern South America to northern Argentina (Tryon & Tryon, 1982). For many *Adiantopsis* species, collection data are not clear enough to determine their modern political districts. For collections that indicate an historical political district with insufficient data to determine its modern location, the historical district is included in the specimens examined lists. Collections lacking data to determine a political district at all are indicated as "unknown" in the specimens examined lists.

Nomenclature. Fée (1852) designated *Adiantopsis paupercula* the type species by unambiguously referencing Kunze's 1850 publication of *Adiantum pauperculum*. However, Christensen (1906) later lectotypified the genus with *A. radiata*. Fée's (1852) original typification is recognized as correct here. For more details, see previous discussion in the Taxonomic History section.

Distinguishing characters. *Adiantopsis* is distinguished from *Cheilanthes* by the following combina-

tion of characters: echinate spore ornamentation (excluding *A. asplenioides*); separate and distinct pseudoindusia, each covering a single sorus; an adaxial pair of golden carinae that occur on all laminar axes and generally on stipes, and which are distinct in color and position from laminar tissue; and finally septate-capitate hairs with distinct, transverse septae and bulbous apical cells, these distributed diffusely on abaxial surfaces of axes and laminar tissue, although often concentrated at axis junctions.

Key to the Species of Caribbean *Adiantopsis*

1a. Lamina palmate . . . . 6. *A. radiata*
1b. Lamina pedate or pinnate.
  2a. Lamina pinnate.
    3a. Pseudoindusia indurated with whitened to pale blue cells; sporangia sessile; lamina once pinnate to bipinnate; ultimate divisions deeply lobed . . . . 1. *A. asplenioides*
    3b. Pseudoindusia not indurated, hyaline to green; sporangia stalked; lamina bipinnate or more compound; ultimate divisions entire to crenulate.
      4a. Laminar apex conform; ultimate divisions with stalk swollen at juncture with laminar tissue . . . . 3. *A. paupercula*
      4b. Laminar apex difform; ultimate divisions without stalk swollen at juncture with laminar tissue.
        5a. Lamina quadripinnate; ultimate divisions less than 3.5 mm long and 2.5 mm wide; fertile divisions strongly revolute . . . . 2. *A. parvisegmenta* (new species)
        5b. Lamina tripinnate or less compound; ultimate divisions more than 3.5 mm long and 2.5 mm wide; fertile divisions more or less flat.
          6a. Carinae beginning in upper quarter of stipe; laminar tissue thin-spongiose to chartaceous; mode of 16 indurated arcus cells . . . . 8. *A. rupicola*
          6b. Carinae beginning at base of or in lower half of stipe; laminar tissue papyraceous; mode of 14 indurated arcus cells.
            7a. Apices of ultimate divisions crenulate; rachis basal diameter 1.1–1.5 mm; ultimate divisions ascending; laminar axes persistent, the costae straight; Jamaica and Hispaniola . . . . 7. *A. reesii*
            7b. Apices of ultimate divisions entire; rachis basal diameter 0.6–1.2 mm; ultimate divisions patent to slightly ascending; laminar axes marcescent, the costae curling acroscopically; Cuba . . . . 9. *A. vincentii* (new species)
  2b. Lamina pedate.
    8a. Apices of ultimate divisions crenulate; carinae beginning in basal half of stipe; mode of 14 annulus cells; ultimate division stalks 0.1–0.6 mm long; ultimate divisions slightly ascending; basal basiscopic pinnules 2.2–5.1 times longer than basal acroscopic pinnule; Jamaica and Hispaniola . . . . . 4. *A. pedata*
    8b. Apices of ultimate divisions acute to round; carinae beginning in apical half of stipe; mode of 16 annulus cells; ultimate division stalks 0.9–6.3 mm long; ultimate divisions more or less patent; basal basiscopic pinnules 1.8–13.1 times longer than basal acroscopic division; Cuba . . . . . 5. *A. pentagona* (new species)

1. Adiantopsis asplenioides Maxon, Amer. Fern J. 22: 14. 1932. TYPE: Cuba. Pinar del Río, Río del Medio, at Las Pozas, very scarce, 10 Sep. 1923, *E. L. Ekman 17456* (holotype, US!). Figure 6A, B.

Rhizome erect, to 1.5 cm long, 0.3–0.8 cm diam.; *scales* bicolorous with an atrocastaneous center and translucent margins, acicular to lanceate (subulate), basifixed, 1.60–5.20 mm long, 0.12–0.55 mm wide, bases truncate, margins entire to slightly repand, apices attenuate. *Fronds* erect, 9.5–18.5 cm long. *Stipes* atrocastaneous to castaneous, never bicarinate adaxially, shorter than lamina, 1.5–4.0 cm long, 0.2–0.6 mm basal diam.; *carinae* absent; *scales* absent; *hairs* rare, septate-capitate or rarely ciliform. *Laminae* pinnate-pinnatifid to bipinnate, linear, drying dull green, 8.0–14.5 cm long, 0.5–1.1 cm wide, apices difform, long attenuate; *laminar tissue* chartaceous, hydathodes marginal in sinuses, surrounded by prominent white to pale blue epidermal cells; *hairs* with basal cell elongate, clear or white, middle cell short, tan or clear, apical cell elongate-bulbous, clear, white, or golden; *stoma* complanate, guard cells 45.64–57.05 μm long. *Laminar axes* persistent, atrocastaneous to castaneous, grading into lamina and taking its color and texture; *rachis* 0.2–0.5 mm basal diam.; *carinae* colored as axis or golden, grading into lamina; *scales* absent. *Pinnae* patent to slightly ascending, 16–20 pairs, alternate, sub-opposite basally, widely rhombiform, obovate, to oblong, slightly inequilateral to equilateral, to 2.7–6.3 mm long, 1.7–6.0 mm wide, apices round to acute. *Ultimate divisions* patent to slightly ascending, articulate, widely rhombic, flabellate, obovate, to oblong, to 2.6–6.3 mm long, 1.5–6.0 mm wide, bases cuneate, margins deeply 2–6 lobed, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.1–0.4 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, obscure to occult. *Pseudoindusia* distinct or confluent across sinuses, reniform to sub-reniform, white to pale blue, occasionally hyaline, 0.50–0.78 mm long, 0.36–0.50 mm wide, margin entire to slightly erose. *Sporangia*

Figure 6. —A. *Adiantopsis asplenioides* (*Bro. Alain 1226 & Acuna*, US). Scale bar = 3.0 cm. —B. Lobed ultimate divisions with indurated pseudoindusia. Scale bar = 0.5 cm. C. *Adiantopsis parvisegmenta* (*C. V. Morton 4166*, US). Scale bar = 3 cm. —D. Small, revolute ultimate divisions of *A. parvisegmenta*. Scale bar = 0.15 cm.

globose, sessile on receptacle, arcus of 11–15 indurated cells, these 30.97–39.12 μm tall. *Spores* 32 per sporangium, tetrahedral-globose, white to pale yellow at maturity, white to pale yellow when immature, 58.68–88.02 μm diam., cristate with anastomosing strands below the muri, laesura not obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. A rare endemic of Pinar del Río and an unknown site in eastern Cuba. Restricted to moist, serpentine soils or rocks. In Pinar del Río, Cuba, the species is found on serpentine mogotes. Although there are few collections of this geographically and edaphically restricted taxon, it is likely still extant in Cuba and protected within the confines of Valle de Viñales and other national parks.

Notes. *Adiantopsis asplenioides* is the only Caribbean *Adiantopsis* to possess cristate, rather than echinate, spores. It shares this trait with some putative South American *Adiantopsis*, such as *Cheilanthes dichotoma* Sw. (Ponce & Morbelli, 1989). The ultimate generic position of these cristate taxa will be determined by ongoing research investigating South American *Adiantopsis* and morphologically similar *Cheilanthes*.

Adiantopsis asplenioides is morphologically similar to an undescribed Bolivian and Paraguayan taxon (Barker, pers. obs.). Both taxa have sessile, globose sporangia, deeply lobed margins, white to pale yellow spores, and prominent white or blue epidermal cells surrounding the hydathodes. These two taxa are distinctive and their relationship with the rest of *Adiantopsis* should be tested with molecular data.

Adiantopsis asplenioides is unique among Caribbean *Adiantopsis* in having 32 large spores per sporangium and indurated pseudoindusia. Although it has the largest spores, this species is likely a diploid, as guard and indurated arcus cell sizes place it among other putative diploid taxa. It is possible that the large spore size and persistent, indurated pseudoindusium are adaptations to restrict spore distribution to the serpentine substrates on which it occurs. The species may also be apogamous, a common cause of reduced spore number.

Selected specimens examined. CUBA. **Pinar del Río**: Loma Zambumbia, Rangel, Sierra del Rosario, *Bro. Alain 6108* (US); La Cajalbana, La Palma, *Acuña & Alain 15787* (US). **Eastern Cuba**: Cuba Orientali, *C. Wright 881* (US).

2. Adiantopsis parvisegmenta M. S. Barker & Hickey, sp. nov. TYPE: Cuba. Las Villas (formerly Santa Clara), Trinidad Mtns., Buenos Aires, rare fern on rocks, alt. 800 m, *C. V. Morton 4166* (holotype, US!; isotypes, GH!, UC!, US!). Figure 6C, D.

Laminae quadripinnatae; segmenta ultima pusilla, 1.9–3.5 mm longa, 1.2–2.5 mm lata. Ab *A. vincentii* segmentis ultimis fertilis valde revolutis et textura spongiosa differt.

Rhizome ascending to decumbent, to 2.5 cm long, 1.2–2.3 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceate to acicular, basifixed, 4.50–6.00 mm long, 0.33–0.50 mm wide, bases truncate, margins entire to slightly repand, apices acute. *Fronds* strict, 54.0–74.0 cm long. *Stipes* atrocastaneous, always bicarinate adaxially, shorter than lamina, 15.5–28.3 cm long, 1.6–2.3 mm basal diam.; *carinae* beginning at stipe base or in the basal ¼ of stipe and continuing into rachis; *scales* extending 1.3–3.4 cm up the stipe, divergent, concolorous, tan, lanceolate to acicular (subulate), pseudopeltate to basifixed, 3.40–4.63 mm long, 0.30–0.48 mm wide, bases biauriculate to truncate, margins entire to slightly repand, apices acute; *hairs* rare, septate-capitate. *Laminae* quadripinnate, triangular to lanceate, drying dull green, 26.3–45.7 cm long, 6.5–28.0 cm wide, apices difform, cuneate to acute; *laminar tissue* spongiose, hydathodes marginal; *hairs* with basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; *stoma* complanate, guard cells 32.60–58.68 μm long. *Laminar axes* persistent, atrocastaneous, grading into lamina and taking its color and texture; *rachis* 1.7–2.3 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, narrowly triangular, 0.65–1.10 mm long, 0.02–0.10 mm wide, bases truncate, apices acute. *Pinnae* ascending, 26–45 pairs, alternate, frequently incurved along basal half of lamina, straight distally, triangular to narrowly triangular, inequilateral, to 8.5–16.5 cm long, 3.3–12.5 cm wide, apices acute to cuneate. *Pinnules* patent to slightly ascending, narrowly triangular, to 1.5–7.5 cm long, 0.5–2.5 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices attenuate to cuneate. *Ultimate divisions* patent to slightly ascending, articulate, ovate, elliptic to oblong, 1.9–3.5 mm long, 1.2–2.5 mm wide, bases cuneate, frequently uniauriculate acroscopically, margins entire, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.2–0.5 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, occult. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.50–0.72 mm long, 0.22–0.48 mm wide, margin erose to slightly erose. *Sporangia* subglobose, long stalked, arcus of (12–)14–25 indurated cells, these 32.60–48.90 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23–47.27 μm diam., echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. A rare endemic in the Escambray mountains of Cienfuegos, Sancti Spiritus, and Villa Clara Provinces, Cuba. *Adiantopsis parvisegmenta* has been collected on rocks, most likely amphibolite at approximately 800 m altitude. Like other *Adiantopsis* taxa, *A. parvisegmenta* is known from very few collections and from one small geographic region. This species appears to be confined to the amphibolitic substrates of the Escambray Mountains, as it has not been found outside of the region. The Trinidad and Valle de los Ingenios National Park and World Heritage site occur in the range of *A. parvisegmenta* and should afford it some protection.

Notes. As its name implies, *Adiantopsis parvisegmenta* is distinguished from most other pinnate taxa by its small ultimate divisions. However, it may be confused with *A. vincentii*, because the ultimate divisions of the two taxa overlap in size. Three characters can be used to reliably distinguish the two species. *Adiantopsis parvisegmenta* has a spongiose lamina in contrast to the papyraceous lamina of *A. vincentii*. The fertile ultimate divisions of *A. parvisegmenta* are strongly revolute, whereas those of *A. vincentii* are more or less flat. Finally, *A. parvisegmenta* is quadripinnate with a generally broader lamina than *A. vincentii*, which is tripinnate and generally narrower. *Adiantopsis parvisegmenta* is most likely a diploid species, based on indurated arcus cell, guard cell, and spore sizes, and may contribute to the parentage of some elements of the putative allotetraploid *A. pentagona*.

It should be noted that specimens of *Adiantopsis parvisegmenta* were frequently determined as *A. reesii*. In folders at US, Proctor noted that these collections were not *A. reesii*, and he was correct. Thus, Cuban material determined as *A. reesii* may be *A. parvisegmenta*, *A. rupicola*, or *A. vincentii*, as these species were frequently included under *A. reesii* by past researchers.

Paratypes. CUBA. **Las Villas:** Las Laguanas, Buenos Aires, *J. G. Jack 6869* (NY), *6877* (US), *7033* (US [2]).

3. Adiantopsis paupercula (Kunze) Fée, Gen. Filic. [Mém. Foug. 5]: 145. 1852. *Adiantum pauperculum* Kunze, Farrnkräuter 2(13): 65. t. 127. 1850. *Cheilanthes paupercula* (Kunze) Mett., Fil. Hort. Bot. Lips. 52. 1856. *Hypolepis paupercula* (Kunze) Hook., Sp. Fil. 2: 73. t. 88-C. 1856. TYPE: Cuba. Oriente, Mt. Líbano, 1844, *J. Linden 1864* (holotype, LZ not seen; isotypes,

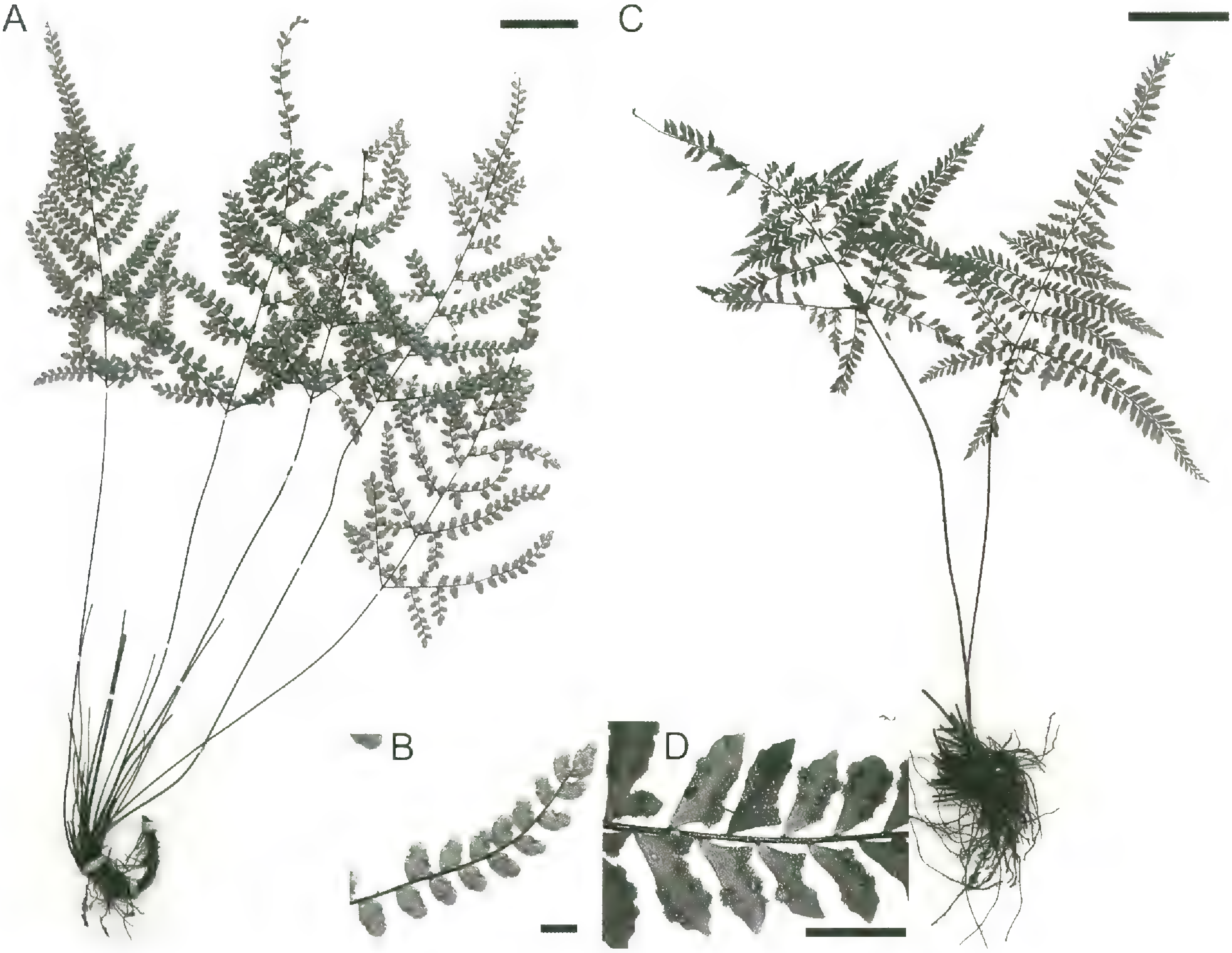

Figure 7. —A. *Adiantopsis paupercula* (*W. R. Maxon 4239*, US). Scale bar = 3 cm. —B. Ultimate divisions of *A. paupercula*. Scale bar = 0.5 cm. —C. *Adiantopsis pedata* (*Wm. Harris 10878*, GH). Scale bar = 3 cm. —D. Ultimate divisions of *A. pedata* with toothed apices. Scale bar = 0.75 cm.

B!, BM!, BM photo US!, K!, L!, P!, US!). Figure 7A, B.

Rhizome decumbent to erect, to 5.9 cm long, 0.3–1.1 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceate to acicular, basifixed, 3.61–13.93 mm long, 0.30–0.87 mm wide, bases truncate, margins entire, apices attenuate. *Fronds* erect, 12.5–65.5 cm long. *Stipes* atropurpureous to atrocastaneous, always bicarinate adaxially, longer than or equal (shorter) to lamina, 8.5–35.5 cm long, 0.4–2.3 mm basal diam.; *carinae* beginning near midpoint of stipe and continuing into rachis; *scales* extending 1.4–6.4 cm up the stipe, divergent, concolorous, tan, lanceate, pseudopeltate to basifixed, 3.2–9.5 mm long, 1.2–5.2 mm wide, bases biauriculate to truncate, margins entire, apices attenuate; *hairs* septate-capitate. *Laminae* tripinnate, bipinnate, to quadripinnate, triangular, drying green to brown, 9.5–30.0 cm long, 4.5–19.0 cm wide, apices conform, attenuate; *laminar tissue* spongiose, hydathodes marginal; *hairs* with basal cell elongate, clear or white, middle cell short, clear, red, or golden, apical cell bulbous, clear, red, or golden; *stoma* complanate, guard cells 48.90–68.46 μm long. *Laminar axes* persistent, atropurpureous to atrocastaneous, not grading into lamina at apices; *rachis* 0.5–1.4 mm basal diam.; *carinae* golden, not grading into lamina; *scales* absent. *Pinnae* ascending to patent, 21–33 pairs, alternate, occasionally incurved in basal half of lamina, straight distally, linear to narrowly triangular, inequilateral, to 3.1–12.4 cm long, 0.9–7.4 cm wide, apices acute to cuneate. *Pinnules* slightly ascending to patent, linear, basal pinnules 1.1–6.0 cm long, 0.5–1.0 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices cuneate to acute. *Ultimate divisions* slightly ascending to patent, strongly articulate, flabellate, rhombiform, to oblong, 3.2–8.0 mm long, 2.5–4.5 mm wide, bases acute to truncate, margins entire, apices round to acute; *stalks* persistent, swollen at junction with laminar tissue, 2.4–4.8 mm long. *Veins* flabellate, immersed in lamina, occult to obscure. *Pseudoindusia* distinct, lunate, hyaline, occasionally black maculate, 0.8–0.9 mm long, 0.25–0.60 mm wide, margin erose. *Sporangia* subglobose, long stalked, arcus of 14–20 indurated

cells, these 35.86–47.27 µm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 35.86–45.64 µm diam., echinate, echinae compact with complete bases, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. Found on the islands of Cuba, Jamaica, and Puerto Rico on shaded, rocky limestone or serpentine slopes and cliffs between 400–1000 m altitude. *Adiantopsis paupercula* is the most widespread endemic Caribbean *Adiantopsis*. This is probably because the species can occur on both limestone and serpentine substrates, whereas other endemic Caribbean *Adiantopsis* appear to have greater substrate specificity. It should be noted that on two recent collecting trips to Puerto Rico *A. paupercula* was not found, and it may no longer be on the island, because it was previously known from only one collection (Proctor, 1989). However, it probably still occurs on Cuba and Jamaica. In Cuba, some of its habitat is protected by the Alejandro de Humboldt National Park and World Heritage site.

Notes. *Adiantopsis paupercula* is one of the more distinctive *Adiantopsis* species. The strongly articulate, flabellate to rhombiform ultimate divisions with a swelling at the junction of the stalk and laminar tissue distinguish this species from other *Adiantopsis*. It is likely a diploid species, because its indurated arcus cell and spore sizes place it within a diploid group of taxa. However, its guard cell sizes are larger than other putative diploids, and it is not clear why.

Selected specimens examined. CUBA. **Guantanamo**: Top of El Yunque, limestone mtn. near Baracoa, *E. L. Ekman 3977* (US); Monte Libanon, San Fernandez, *E. L. Ekman 10308* (B, US). **Holguin**: Mina Cayoguan, *Bro. Clement 3982* (US); Vedado-Habana, Banks of Cayoguan River N of Sierra de Moa, *Fres Lein 20910, M. Victorin, Clement* (US); Sierra de Nipe, headwaters of Pilots River, *E. L. Ekman 2515* (B, BM, US); Camp La Gloria, S of Sierra Moa, *J. A. Shafer 8174* (K, US); Sierra Nipe, near Woodfred, Rocky Arroyos, *J. A. Shafer 3169* (K, MO, US); Sierra de Nipe, Loma Monsura, NW side of top, *E. L. Ekman 5746* (US); Sierra Nipe, along Rio Medio near Woodfred, *C. V. Morton 4526, Julian Acuna* (US); Vedado Habana, Pena Prieta, *Bro. Alain 3583* (US). **Oriente**: Mt. Libano, *J. Linden 1862* (K); Monte Libano, caverns of Thermopylae & vic., *W. R. Maxon 4239* (P, US [2]); Monte Verde, *C. Wright 962* (UC); Monte Verde, *C. Wright 964* (BM [2], K [3], L, MO, US [3]).

JAMAICA. **Clarendon**: Peckham Woods, *W. Harris 11021* (BM, US); Peckham Woods, *W. Harris 12771* (BM, K [2], MO, US); Peckham Woods, *W. T. Stearn 17* (BM). **Portland**: E slope of John Crow Mtns. ca. 2.5 mi. SW of Ecclesdown, *G. R. Proctor 5729* (MO). **St. Ann**: Douglas Castle District, ca. 2 mi. NW of Mason River Savanna, *A. M. Evans 2349* (BM). **Trelawny**: On limestone cliffs, *L. M. Underwood 3304* (US, P); Six mi. WNW of Troy on Crown Lands Road, *H. A. Hespenheide 1191, E. B. Hespenseide, J. S. Calver, R. E. Ricklefs* (DUKE, UC, US); Crown Lands Road extension ca. 5 mi. NW of Troy, *G. R. Proctor 31099* (DUKE); 4 mi. WNW of Troy on Crown Lands Road, *H. A. Hespenheide 1180* (DUKE); On limestone rocks, *L. M. Underwood 3303* (US); Near Troy, *W. Harris 8791* (BM).

PUERTO RICO. **Maricao**: Maricao State Forest, Barrio Tabonuco, headwaters stream of Rio Seco, below Road 120, km. 10.15, *G. R. Proctor 41649* (US).

4. **Adiantopsis pedata** (Hook.) T. Moore, Ind. Fil. 18. 1857. *Hypolepis pedata* Hook., Sp. Fil. 2: 73, t. 92-A. 1852. *Cheilanthes pedata* (Hook.) A. Braun, Index Seminum. 1857. TYPE: Jamaica. *Purdie s.n.* (holotype, K!, K photo B!, K photo MICH!; isotypes, BM!, BM photo B!, BM photo MICH!, P!). Figure 7C, D.

Rhizome erect to decumbent, to 3.0 cm long, 0.6–1.4 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceate, basifixed, 3.50–4.75 mm long, 0.43–0.45 mm wide, bases truncate, margins entire, apices acute. *Fronds* strict, 21.7–32.3 cm long. *Stipes* atropurpureous to atrocastaneous, always bicarinate adaxially, longer than or equal to lamina, 11.3–19.0 cm long, 0.8–1.3 mm basal diam.; *carinae* beginning at stipe base or in the basal ½ of stipe and continuing into rachis; *scales* extending 2.3–3.4 cm up the stipe, appressed, concolorous, tan, lanceolate, pseudopeltate, 3.50–4.00 mm long, 0.53–0.58 mm wide, bases biauriculate, margins entire to slightly repand, apices acute; *hairs* rare, septate-capitate. *Laminae* pedate, tripinnate to rarely quadripinnate basally, abruptly bipinnate above, broadly deltate-pentagonal, drying yellow-green, green, dark green to brown, 8.5–19.4 cm long, 9.4–25.7 cm wide, apices difform, attenuate; *laminar tissue* chartaceous, hydathodes marginal; *hairs* with basal cell elongate and clear, middle cell frequently short and red, golden red, golden, or white, apical cell bulbous and clear, white, or golden; *stoma* complanate, guard cells 53.79–78.24 µm long. *Laminar axes* persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *rachis* 0.4–1.0 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, linear, 0.45–0.88 mm long, 0.02–0.07 mm wide, bases truncate, apices acute. *Pinnae* ascending to patent, 21–28 pairs, basal pinnae opposite to sub-opposite, straight, triangular, inequilateral, to 4.7–12.9 cm long, 1.7–6.0 cm wide, apices attenuate to acute; penultimate pinnae opposite to sub-opposite, narrowly fusiform to linear, abruptly shorter, 2.5–7.1 cm long; distal pinnae alternate, quickly reduced in length. *Pinnules* patent to slightly ascending, linear, apices attenuate to cuneate; *basal basiscopic pinnules* of basal pinnae narrowly triangular to fusiform, much extended, 1.0–5.6 cm long, 2.2–5.1 times longer than basal acroscopic pinnule, basal

acroscopic pinnule 0.5–1.3 cm long, distal pinnules of first pinnae equivalent, abruptly shorter than basal basiscopic pinnule. *Ultimate divisions* ascending, articulate, oblanceolate, narrowly elliptic, to narrowly oblong, 4.0–9.0 mm long, 1.4–3.5 mm wide, bases cuneate, uniauriculate acroscopically, margins entire proximally, crenulate distally, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.10–0.60 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, occult to obscure. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.60–0.84 mm long, 0.30–0.56 mm wide, margin slightly erose. *Sporangia* subglobose, long stalked, arcus of 13–15(–20) indurated cells, these 40.75–55.42 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 38.31–54.61 μm diam., densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. *Adiantopssis pedata* is a rare fern known only from the Dominican Republic and Jamaica. The species has been collected in humus on wooded hillsides scattered with limestone rocks at 800–1000 m altitude. Although no recent collections have been made, it occurs in very rural areas that have relatively little economic development, such as the Cockpit Country of Jamaica. Given that ecotourism is becoming an industry in this part of Jamaica, the habitat of *A. pedata* is likely to be preserved, and the species may still be found there if collections are sought.

Notes. *Adiantopsis pedata* formerly included plants from Cuba. However, the Cuban material recognized here as *A. pentagona* is clearly distinct. Carinae beginning in the basal half of the stipes, generally ascending ultimate divisions with crenulate apices, and a mode of 14 indurated arcus cells distinguish *A. pedata*. *Adiantopsis pentagona* has carinae beginning in the apical half of the stipes, patent or slightly ascending ultimate divisions, entire or only slightly crenulate ultimate division apices, and a mode of 16 indurated arcus cells. Both Caribbean taxa may be confused with the South American *A. ×australopedata*, which is a sterile hybrid that occurs in the tri-border region of Argentina, Brazil, and Paraguay. The aborted spores, crenulate margins, and generally much larger frond size distinguish *A. ×australopedata* from the Caribbean taxa (Hickey et al., 2003).

Adiantopsis pedata appears to be a tetraploid derivative of *A. radiata* and *A. reesii*. Indurated arcus cell, guard cell, and spore sizes strongly suggest that it is tetraploid. Its pedate morphology suggests that it is a hybrid taxon, with *A. radiata* as one parent (Hickey et al., 2003). Also shared with *A. radiata* are spore echinae that are basally dissected, and a common pattern of laminar development. With *A. reesii*, *A. pedata* shares distinctly toothed ultimate division apices, a mode of 14 indurated arcus cells, and carinae beginning in the lower portions of the stipe. Based on all these data, *A. pedata* is supported as a tetraploid derivative of *A. radiata* and *A. reesii*. Future cytological research needs to be conducted to confirm its ploidy level, and future molecular research should test the parentage of *A. pedata*.

Selected specimens examined. DOMINICAN REPUBLIC. **Monte Cristi**: Cordillera Central, Monción, *E. L. Ekman 12693* (B, BM, K, US [2]).

JAMAICA. **Clarendon**: Peckham Woodland, *W. Harris 10,878* (B, GH, K, US [2]); Glenwood Springs, along road between Balcarres & Sunbury, *G. R. Proctor 35655* (US). **Unknown Parish**: Jamaica, *Walker-Arnott s.n.* (NY).

5. Adiantopsis pentagona M. S. Barker & Hickey, sp. nov. TYPE: Cuba. Santa Clara, vic. of Sopapo, Buenos Aires, Trinidad Mtns., shaded limestone cliff, 4 Aug. 1936, *L. B. Smith 3320, A. R. Hodgdon, & F. Gonzalez* (holotype, GH!; isotypes, NY!, US!). Figure 8A, B.

Laminae pedatae; pinnae supernae bipinnatae; pinnae basales tripinnatae, pinnulis valde basalibus elongatis magnopere. Ab *A. pedata* carinis in dimidio superno stipitis exorientibus, segmentis ultimis patentibus vel leviter ascendentibus praebentibus apices integros vel leviter crenulatos, arcu e cellulis induratis 16 (modus) composito, et ab *A. ×australopedata* sporis fertilibus (nonabortivis) differt.

Rhizome erect to decumbent, to 3.8 cm long, 0.5–1.8 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, acicular to lanceate, basifixed, 2.13–7.58 mm long, 0.08–0.88 mm wide, bases truncate, margins repand to entire, apices acute. *Fronds* strict, 33.2–72.1 cm long. *Stipes* atropurpureous to atrocastaneous, always bicarinate adaxially, longer than or equal to lamina, 17.1–44.0 cm long, 0.8–2.1 mm basal diam.; *carinae* beginning in the upper ⅓ (½) of stipe and continuing into rachis; *scales* extending 2.0–3.7 cm up the stipe, appressed, concolorous, tan, acicular to lanceate (subulate), pseudopeltate, 1.05–6.38 mm long, 0.13–0.83 mm wide, bases biauriculate, margins entire to slightly repand, apices acute; *hairs* rare, septate–capitate. *Laminae* pedate, tripinnate to quadripinnate basally, abruptly bipinnate above, broadly deltate-pentagonal, drying brown, dark green, green to yellow-green, 14.7–28.1 cm long, 12.8–48.2 cm wide, apices difform, long attenuate; *laminar tissue* thin-spongiose,

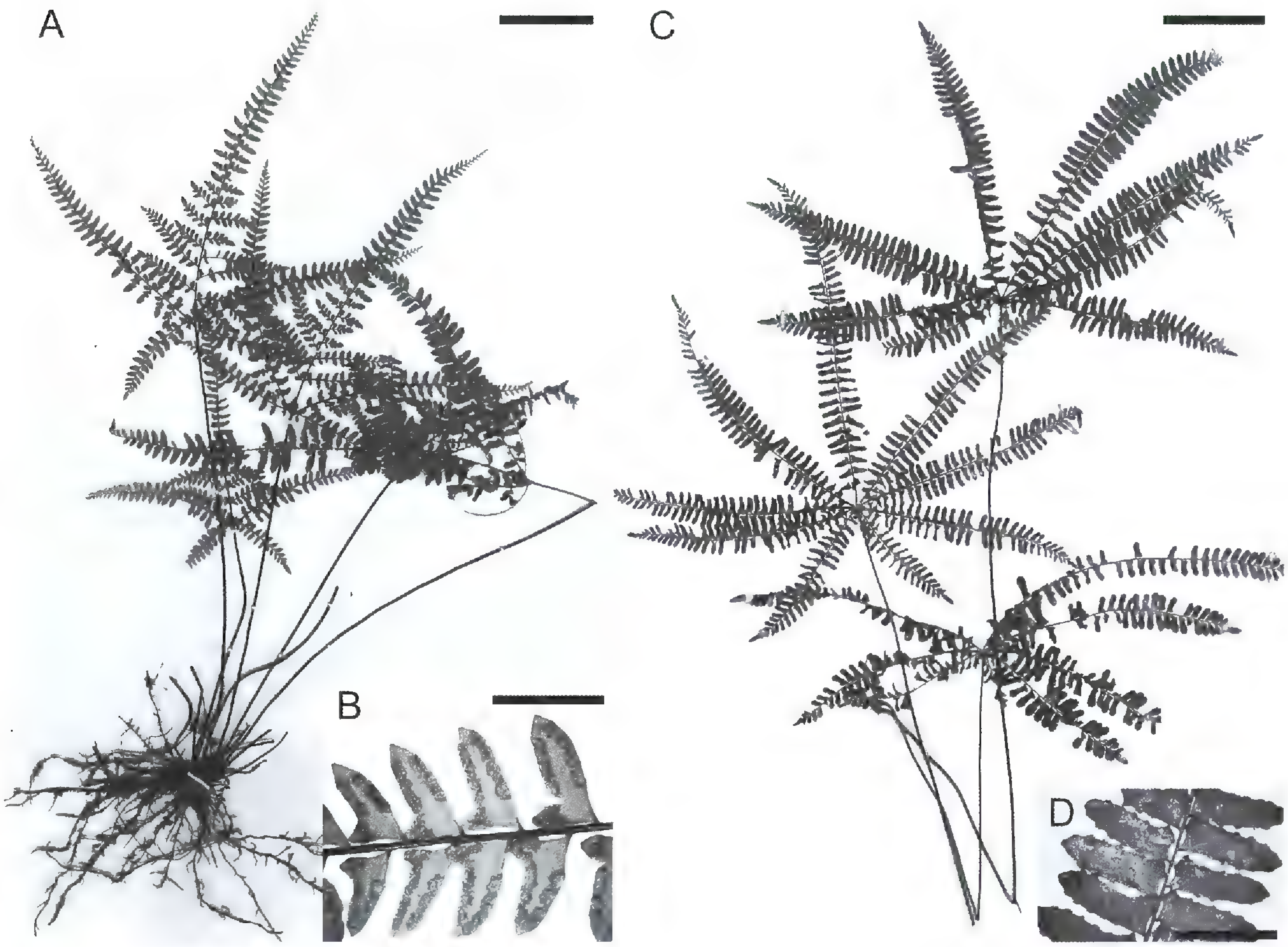

Figure 8. —A. *Adiantopsis pentagona* (*L. B. Smith 3320 et al.*, US). Scale bar = 3 cm. —B. Ultimate divisions of *A. pentagona* without toothed apices. Scale bar = 0.75 cm. —C. *Adiantopsis radiata* (*G. R. Proctor 29256*, F). Scale bar = 3 cm. —D. Ultimate divisions of *A. radiata*. Scale bar = 0.75 cm.

hydathodes marginal; *hairs* with basal cell elongate and clear, middle cell frequently short and white, golden, golden red, or red, apical cell bulbous and clear, white, or golden; *stoma* complanate, guard cells 48.90–83.13 μm long. *Laminar axes* persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *rachis* 0.5–1.3 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, lanceate to linear, 0.77–1.45 mm long, 0.08–0.17 mm wide, bases truncate, apices attenuate. *Pinnae* patent to ascending, 28–40 pairs, basal pinnae opposite to sub-opposite, straight, triangular, inequilateral, to 6.4–24.1 cm long, 2.8–19.9 cm wide, apices attenuate to acute; penultimate pinnae sub-opposite, linear, abruptly shorter, 1.4–14.2 cm long; distal pinnae alternate, quickly reduced in length. *Pinnules* patent to slightly ascending, linear to narrowly lanceate, apices cuneate to attenuate; *basal basiscopic pinnules* of basal pinnae fusiform to narrowly triangular, much extended, 1.8–15.3 cm long, 1.8–13.1 times longer than basal acroscopic pinnule, basal acroscopic pinnule 0.4–5.8 cm long, distal pinnules of first pinnae equivalent, abruptly shorter than basal basiscopic pinnule. *Ultimate divisions* patent to slightly ascending, articulate, narrowly oblong, oblanceolate, lanceolate, to narrowly elliptic, 6.1–11.1 mm long, 2.5–4.2 mm wide, bases cuneate, frequently uniauriculate acroscopically, margins entire to slightly crenulate, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.9–6.3 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, occult to obscure. *Pseudoindusia* distinct, lunate to quadrangular, hyaline with a brown or black area proximally where hydathode terminates, occasionally black maculate, 0.35–1.10 mm long, 0.20–0.60 mm wide, margin entire to slightly erose. *Sporangia* subglobose, long stalked, arcus of 14–22 indurated cells, these 40.75–58.68 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 40.75–58.90 μm diam., densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. A Cuban endemic found in the province of Pinar del Río, and the Escambray Mountains of Cienfuegos, Sancti Spiritus, and Villa Clara. *Adiantopsis pentagona* has been collected on moist, shaded limestone or amphibolite soils, rocks,

cliffs, and cave entrances. When *A. pentagona* has been collected in soil, it was generally found on slopes scattered with limestone or amphibolite rocks. *Adiantopsis pentagona* is most likely still found in Cuba. In Pinar del Río, it is probably protected within the boundaries of Valle de Viñales National Park, and by the Trinidad and Valle de los Ingenios National Park in the Escambray Mountains.

Notes. *Adiantopsis pentagona* is named for the overall pentagonal outline of the lamina. *Adiantopsis pedata* and *A.* ×*australopedata* also have pentagonal laminar outlines and may be confused with *A. pentagona*. Carinae beginning in the basal half of the stipes, distinctly crenulate ultimate division apices, generally ascending ultimate divisions, and mode of 14 indurated arcus cells, distinguish *A. pedata* from *A. pentagona*, which has carinae beginning in the apical half of the stipe, entire or slightly crenulate ultimate division apices, patent to slightly ascending ultimate divisions, and a mode of 16 indurated arcus cells. *Adiantopsis* ×*australopedata*, a hybrid distributed in the tri-border region of Argentina, Brazil, and Paraguay, may be distinguished from the Caribbean species by its aborted spores, crenulate margins, and generally larger laminae.

Adiantopsis pentagona appears to be the allotetraploid derivative of *A. radiata* and *A. rupicola*. The large spores, guard cells, and indurated arcus cells relative to putative diploid taxa, such as *A. radiata* and *A. rupicola*, suggest that *A. pentagona* is a tetraploid. Its pedate morphology suggests that it is a hybrid taxon, with *A. radiata* as one parent (Hickey et al., 2003). Also shared with *A. radiata* are spore echinae that are basally dissected, and a common pattern of laminar development. With *A. rupicola*, *A. pentagona* shares carinae beginning in the apical portion of stipes, a mode of 16 indurated arcus cells, and the overall ultimate division shape agrees most favorably with *A. rupicola*. The type of *A. pentagona*, *Smith 3320 et al.*, was selected in part because its morphology supports an allotetraploid origin involving *A. radiata* and *A. rupicola*. However, some collections of *A. pentagona*, specifically those with relatively small ultimate divisions that are revolute when fertile suggest that *A. parvisegmenta* may be the parent of a second, cryptic species. This putative cryptic species has been retained in *A. pentagona* because the available data do not clearly differentiate it. Future molecular research should encompass the morphological range of *A. pentagona* and include *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*, to evaluate if cryptic elements are included.

Paratypes. CUBA. **Las Villas:** Las Vegas de Matagua, Trinidad Mtns., *C. V. Morton 10547* (DUKE, US), *C. V. Morton 10799* (BM, DUKE, US [2]); Las Vegas de Matagua, Buenos Aires, *J. G. Jack 7903* (GH [2], NY, US); On the crest of Pico Petrerillo, Trinidad Mtns., *Bro. Alain 6715* (MICH, US); Buenos Aires, Trinidad Mtns., *C. V. Morton 4179* (GH, UC, US); Sierra del Bibisial, Loma de Ponciano, Sancti-Spiritus Mtns., *F. Leon 6712, F. Clement* (NY); San Blas-Buenos Aires, Trinidad Mtns., gulley behind Gavinas, *R. A. Howard 6505* (GH, MO); Trinidad Mtns., *Glen Ames 11.178* (MICH); Deep limestone cave near San Jose, *R. A. Howard 5151* (GH, MO, NY [2]); Buenos Aires, *Roig 6124, Acuna* (NY); Hanabanilla Falls, *R. Howard 146, W. Briggs, P. Kamb, I. Lane, R. Ritland* (GH); San Blas, Naranjal, Trinidad Mtns., *R. A. Howard 5387* (GH, MO, NY); Pitajones, *J. A. Shafer 12204* (GH [2], NY); San Blas-Buenos Aires, Trinidad Mtns., roadsides near Mina Carlota, *A. Gonzales 513* (BM, GH, US); San Blas-Buenos Aires, Trinidad Mtns., Gavinas, *R. A. Howard 6539* (GH); Las Lagunas, Buenos Aires, *J. G. Jack 6869* (US); Buenos Aires, Trinidad Hills, *J. G. Jack 7773* (US). **Pinar del Río**: Sierra de las Animas, *E. L. Ekman 10510* (NY, US). **Sancti Spiritus**: Mogote Caburni, *P. Acevedo-Rdgz., 6461 R. Oviedo, M. Fernandez, N. Vera* (US). **Unknown Province**: *C. Wright 3947* (B); *C. Wright 3949* (GH, K, NY [2]); 1867, c. l. bos. Desd. *s.n.* (FI).

6. **Adiantopsis radiata** (L.) Fée, Gen. Filic. [Mém. Foug. 5]: 145. 1852. *Adiantum radiatum* L., Sp. Pl. 2: 1094. 1753. *Cheilanthes radiata* (L.) John. Smith, J. Bot. (Hooker) 4: 159. 1841. *Hypolepis radiata* (L.) Hook., Sp. Fil. 2: 72. 1852. TYPE: *Sloane "Adiant. 3 radiatum"* (lectotype, LINN 1252.1, chosen by Lellinger, Mem. New York Bot. Gard. 23: 3. 1972). Figure 8C, D.

Rhizome erect, to 3.3 cm long, 0.5–0.9 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceolate to acicular, pseudopeltate to basifixed, 3.75–4.43 mm long, 0.41–0.58 mm wide, bases cordate to truncate, margins repand, apices acute to acuminate. *Fronds* strict, 19.7–62.3 cm long. *Stipes* atropurpureous to atrocastaneous, rarely bicarinate adaxially, longer than lamina, 10.5–47.0 cm long, 0.8–2.0 mm basal diam.; *carinae* when present, beginning at stipe base and continuing into lamina; *scales* extending 0.2–3.5 cm up the stipe, appressed, bicolorous with broad castaneous to tan center and golden margins, or conconlorous, tan, lanceolate, pseudopeltate, 3.00–5.50 mm long, 0.45–0.75 mm wide, bases biauriculate, margins repand, apices acute; *hairs* rare, septate-capitate. *Laminae* palmate, radially bipinnate, orbiculate, geniculate, drying olive-green, dark green, black, to yellow green, 10.2–26.3 cm long, 4.4–25.8 cm wide, apices difform, acute; *laminar tissue* thin-spongiose, hydathodes marginal; *hairs* with basal cell elongate and clear, middle cell frequently short and golden or red, apical cell bulbous and clear or white; *stoma* complanate, guard cells 35.86–63.57 μm long. *Laminar axes* persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *carinae* golden, grading into lamina;

scales absent. *Pinnae* spreading radially from stipe apex, 3–9, straight, linear to narrowly fusiform, apices acute; central pinna to 9.2–15.3 cm long, 1.4–2.7 cm wide; basal pinna to 2.6–9.2 cm long, 1.0–2.2 cm wide; *basal flabellate divisions* often fertile, attached to the stipe apex between pinnae. *Ultimate divisions* patent to ascending, articulate, oblong to narrowly oblong, 6.0–13.5 mm long, 2.1–3.7 mm wide, bases cuneate to acute, margins entire to crenulate, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 1.0–6.0 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, obscure to occult. *Pseudoindusia* distinct, lunate to quadrangular, hyaline, occasionally black maculate, 0.4–0.84 mm long, 0.22–0.56 mm wide, margin entire to slightly erose. *Sporangia* subglobose, long stalked, arcus of 16–27 indurated cells, these 30.97–46.46 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23–47.27 μm diam., densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* $n = 30$.

Distribution and habitat. *Adiantopsis radiata* is by far the most common and widely distributed *Adiantopsis* species. The species is widespread throughout tropical America and occurs from the Caribbean and Mexico south to Argentina. It has most often been collected on moist, calcareous or serpentine, rocky, wooded slopes and has also been collected on limestone cliffs and walls.

Notes. *Adiantopsis radiata* is the most distinctive *Adiantopsis* species, as it is the only palmate species. As the name implies, the pinnae radiate outward from a single point at the stipe apex. Young *A. radiata* may be confused with young *A. pedata* and *A. pentagona* because all three taxa share a similar ternate juvenile form. The most reliable character to distinguish these taxa is indurated arcus cell number. *Adiantopsis radiata* has a mode of 20 indurated arcus cells, whereas *A. pedata* possesses a mode of 14 and *A. pentagona* has a mode of 16. Also, the stipes of *A. radiata* are typically lacking carinae, whereas both *A. pedata* and *A. pentagona* stipes are always adaxially bicarinate. Another character that is useful for distinguishing *A. radiata* and *A. pedata* is ultimate division shape and orientation. The ultimate divisions of *A. radiata* are usually oblong with rounded apices and are generally patent. *Adiantopsis pedata* ultimate divisions are more frequently oblanceolate with a distinctly toothed apex and are ascending.

Adiantopsis radiata is implicated in an interesting pattern of reticulate and morphological evolution. The species apparently hybridizes with various pinnate taxa to produce pedate derivatives. In the Caribbean, these hybrid derived pedate taxa are *A. pedata* and *A. pentagona*, and in South America *A. ×australopedata* (Hickey et al., 2003).

Selected specimens examined. CUBA. **Oriente**: Deciduous woods near base of Loma Menqura, *J. A. Shafer 3777* (F); Monte Verde, *C. Wright 963* (F, MO [2]). **Unknown province**: 1889, *Eggers 4813* (F).

JAMAICA. **Clarendon**: Peckham Woods, *G. R. Proctor 8445* (MO); Peckham Woodland, *W. Harris 10860* (F); Summit area of Crofts Mtn., *G. R. Proctor 29256* (F). **Portland**: 1906, *A. Moore* (MICH). **Trelawny**: Vic. of Troy, *W. R. Maxon 2954* (MICH). **Unknown Parish**: 1886, *J. P. 390* (MO); *W. Harris 9163* (MO).

LESSER ANTILLES. **Dominica**: Cliffs in woodlands on the North River watershed, W slopes of Morne Brule, Portsmouth, *W. H. Hodge 72* (MO [2]); St. Paul, Morne Cola Anglais, *G. L. Webster 13425* (MICH, MO). **Martinique**: 1868, *Sidier s.n.* (F). **Montserrat**: Cudjor Lerad, *J. A. Shafer 453* (F). **Guadeloupe**: Falaises de la rivière des Pères, *Blanchau s.n.* (F). **Unknown Island**: 1881, *J. L. Main s.n.* (MU).

TRINIDAD. 1877–1878, *A. Fendler 7* [herb. chas. *H. Ford 1354*] (F, MICH, MO); Blanchissense Road near Verdant Vale on Banks Main Road, *A. Hambersley s.n.* (F).

7. **Adiantopsis reesii** (Jenm.) C. Chr., Ind. Fil. 22. 1905. *Cheilanthes reesii* Jenm., J. Bot. Brit. For. 24: 267. 1886. TYPE: Jamaica. St. Elizabeth Parish, Oxford, *Rev. T. L. Rees s.n.* (holotype, K!, K photo US!; isotype, BM!, BM photo US!). Figure 9A, B.

Rhizome decumbent to ascending, to 2.8 cm long, 0.6–0.8 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceate to acicular, basifixed, 4.05–5.50 mm long, 0.52–0.61 mm wide, bases truncate, margins slightly repand, apices acute. *Fronds* strict, 17.1–60.0 cm long. *Stipes* atrocastaneous, always bicarinate adaxially, much shorter than lamina, 2.2–22.0 cm long, 1.0–2.6 mm basal diam.; *carinae* beginning at stipe base or in the basal ¼ of stipe and continuing into rachis; *scales* extending 1.9–4.2 cm up the stipe or to the rachis, divergent, concolorous, tan, lanceate to acicular (subulate), pseudopeltate, 1.25–5.75 mm long, 0.20–0.74 mm wide, bases cordate, margins entire to slightly repand, apices acute; *hairs* rare, septate-capitate. *Laminae* tripinnate, lanceolate to narrowly triangular, drying dull green, 5.0–53.0 cm long, 5.5–14.6 cm wide, apices difform, attenuate to acuminate; *laminar tissue* papyraceous, hydathodes marginal; *hairs* with basal cell elongate and clear, middle cell frequently short and clear, brown, or red, apical cell bulbous and frequently covering middle cell, white, clear, or golden; *stoma* impressed, guard cells 32.60–53.79 μm long. *Laminar axes* persistent, atrocastaneous, grading into lamina and taking its

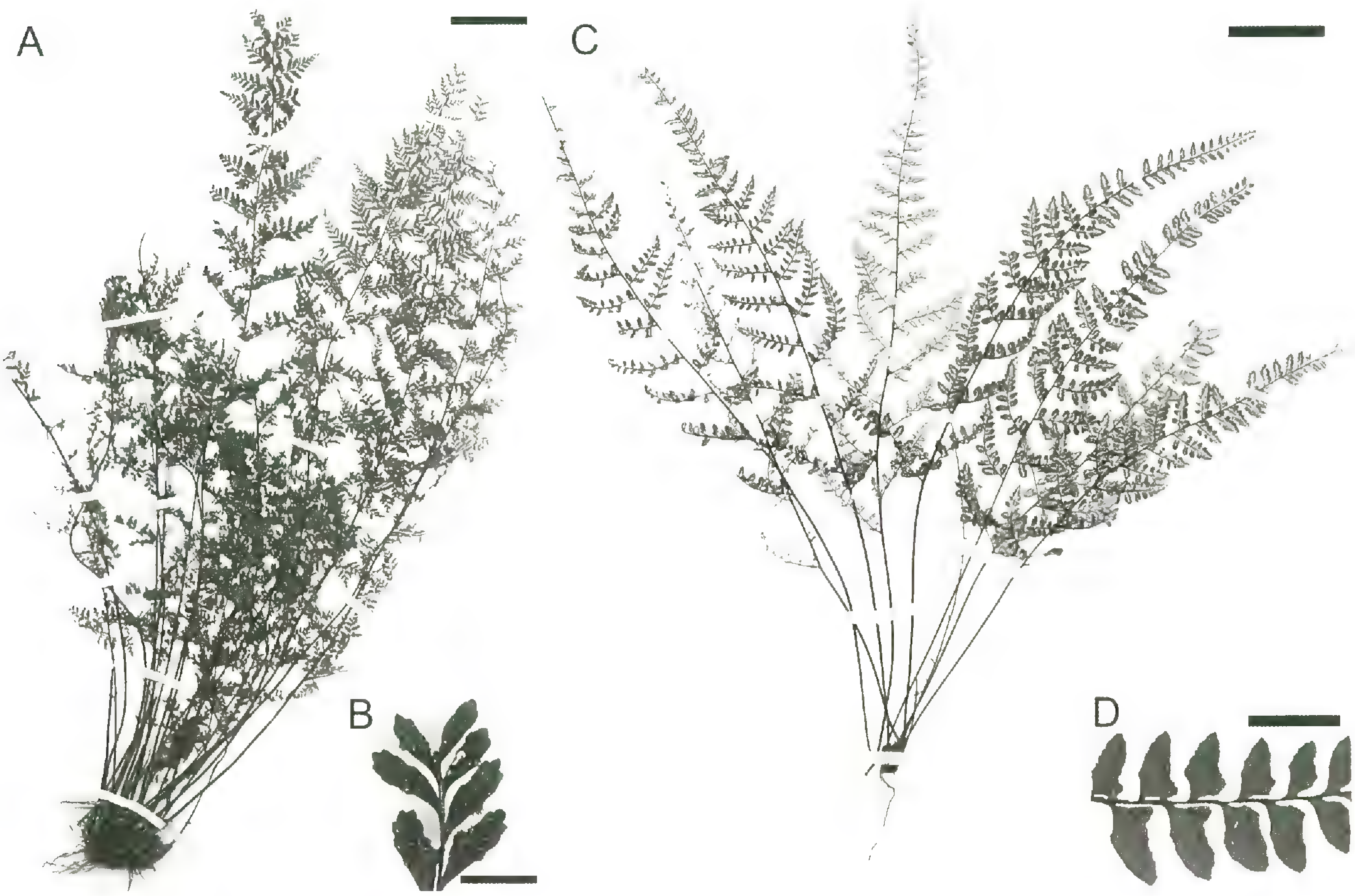

Figure 9. —A. *Adiantopsis reesii* (*E. L. Ekman 9987*, F). Scale bar = 3 cm. —B. Ultimate divisions of *A. reesii* with toothed apices. Scale bar = 0.25 cm. —C. *Adiantopsis rupicola* (*Britton 7497 et al.*, US). Scale bar = 3 cm. —D. Ultimate divisions of *A. rupicola*. Scale bar = 0.75 cm.

color and texture; *rachis* 1.1–1.5 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, narrowly rhombic to lanceolate, 0.70–1.60 mm long, 0.05–0.19 mm wide, bases acute, apices acute. *Pinnae* ascending, 23–55 pairs, alternate, slightly incurved in basal half of lamina, straight distally, narrowly triangular to linear, slightly inequilateral to equilateral, to 5.7–8.2 cm long, 1.8–3.7 cm wide, apices cuneate to acuminate. *Pinnules* ascending to slightly ascending, narrowly triangular to narrowly lanceate, to 1.2–2.3 cm long, 0.7–1.10 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices obtuse to acute. *Ultimate divisions* ascending, articulate, narrowly oblong, oblanceolate, to nearly flabellate, 3.4–9.1 mm long, 1.2–3.8 mm wide, bases cuneate, margins entire to crenulate proximally, crenulate distally, apices round, acuminate to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.3–0.6 mm long. *Veins* pseudodichotomous, anadromous, impressed to immersed in lamina, prominent. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.44–0.92 mm long, 0.30–0.44 mm wide, margin erose to entire. *Sporangia* subglobose, long stalked, arcus of 9–17(–23) indurated cells, these 21.19–48.90 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 30.97–44.83 μm diam., echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. *Adiantopsis reesii* occurs on the islands of Hispaniola and Jamaica. It has been collected on shaded limestone cliffs and slopes, at up to 900 m altitude. Like many other *Adiantopsis* species, *A. reesii* is known from only a few collections and appears to be rare. However, the species is probably still extant, because it occurs in rural areas with little economic development. Additionally, recent ecotourism business in the Cockpit Country of Jamaica may protect its habitat from economic development.

Notes. *Adiantopsis reesii* is distinctive in its toothed ultimate division apices that distinguish it from other pinnate *Adiantopsis*. Further, the ultimate divisions of *A. reesii* are rather elongate compared to other pinnate taxa such as *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*.

Adiantopsis reesii is a putative diploid, as evidenced by the sizes of its guard cells, spores, and indurated arcus cells. This species appears to be one diploid parent, along with *A. radiata*, of the putative tetraploid *A. pedata*. The distinctly toothed apices and ascending

ultimate divisions of *A. reesii* are evident in *A. pedata*. Future molecular research should examine this hypothesized relationship.

Selected specimens examined. HAITI. **Grand' Anse:** Massif de la Hotte, gr. Morne Rockhelois, Meragoaire, at Trou-Gorie, *E. L. Ekman 9987* (BM, F [2], NY, UC, US); Massif de la Hotte, W group, Tiburon, Morne Sentier, *E. L. Ekman 10608* (K, US); Massif de la Hotte, gr. M. Rockhelois, Meragoaire, *Ekman 7965* (US).

JAMAICA. **Trelawny**: Cockpit Country ca. 5 mi. N of Quick Step, above Aberdeen P.O., *G. R. Proctor 4090* (US). **Unknown Parish**: *R. V. Sherring s.n.* (BM).

8. Adiantopsis rupicola Maxon, Contr. U.S. Natl. Herb. 10: 485. 1908. TYPE: Cuba. Pinar del Rio, collected in mtns. near El Guama, crevices of partially shaded cliffs, limestone, rare, *W. Palmer 242 & J. H. Riley* (holotype, US!; isotypes, K!, MO!, US!). Figures 9C, D.

Rhizome ascending to decumbent, to 2.2 cm long, 0.6–1.2 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, acicular to linear, basifixed, 1.60–3.60 mm long, 0.30–0.36 mm wide, bases truncate, margins slightly repand, apices acute. *Fronds* strict, 23.5–50.2 cm long. *Stipes* atropurpureous to atrocastaneous, occasionally bicarinate, shorter than lamina, 4.0–17.5 cm long, 0.6–1.7 mm basal diam.; *carinae* when present, beginning in upper ¼ of the stipe and continuing into the rachis; *scales* extending 1.9–7.1 cm up the stipe, divergent, concolorous, tan, acicular to lanceate, pseudopeltate to basifixed, 1.00–6.64 mm long, 0.06–0.70 mm wide, bases biauriculate to truncate, margins slightly repand to entire, apices attenuate; *hairs* septate-capitate. *Laminae* tripinnate, narrowly triangular to lanceate, drying dull green to brown, 11.0–39.5 cm long, 4.2–17.5 cm wide, apices difform, attenuate; *laminar tissue* thin-spongiose to chartaceous, hydathodes marginal; *hairs* with basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; *stoma* complanate, guard cells 42.38–57.05 μm long. *Laminar axes* marcescent with costae curling acroscopically, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *rachis* 0.6–1.5 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, narrowly lanceolate, 0.67–1.12 mm long, 0.08–0.16 mm wide, bases acute, apices attenuate. *Pinnae* ascending, 21–24 pairs, alternate, frequently incurved in basal half of lamina, straight distally, narrowly triangular, slightly inequilateral to equilateral, to 3.2–16.0 cm long, 0.9–5.5 cm wide, apices acute to attenuate. *Pinnules* patent to slightly ascending, narrowly triangular to linear, basal pinnules 0.7–3.9 cm long, 0.5–1.5 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices acute. *Ultimate divisions* slightly ascending to patent, articulate, oblong to trullate, 3.8–9.5 mm long, 2.0–5.5 mm wide, bases acute to cuneate, frequently uniauriculate acroscopically, margins entire, apices acute to round; *stalks* persistent, not swollen at junction with laminar tissue, 0.1–0.5 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, occult to obscure. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.42–0.70 mm long, 0.30–0.40 mm wide, margin erose to slightly erose. *Sporangia* subglobose, long stalked, arcus of 12–21 indurated cells, these 32.6–42.38 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23–40.75 μm diam., echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. *Adiantopsis rupicola* is endemic to the province of Pinar del Río, Cuba. The species has been collected on shaded, rocky limestone slopes or cliffs. Similar to other *Adiantopsis* taxa, *A. rupicola* is known from few collections. Although there are no recent collections of *A. rupicola*, it probably still occurs in Pinar del Río and is likely protected within the boundaries of Valle de Viñales National Park.

Notes. *Adiantopsis rupicola* may be confused with *A. vincentii*. The carinae of *A. rupicola* begin in the apical quarter of the stipes, whereas the carinae of *A. vincentii* begin in the basal half of the stipes. Also, *A. rupicola* has a mode of 16 indurated arcus cells, whereas *A. vincentii* has a mode of 14. The generally smaller, obovate to oblong ultimate divisions and lanceate to lanceolate lamina of *A. vincentii* also distinguish it from *A. rupicola*, which has generally larger ultimate divisions that are trullate to oblong and a narrowly triangular to lanceate lamina. Additionally, *A. vincentii* appears to be hemi-dimorphic with smaller sterile fronds, whereas *A. rupicola* shows no signs of dimorphism.

Guard cell, spore, and indurated arcus cell sizes place *Adiantopsis rupicola* in a group of putative diploid species. This species may be a parent, along with *A. radiata*, of some component of the putative tetraploid *A. pentagona*. The overall ultimate division shape of *A. pentagona* resembles the generally trullate divisions of *A. rupicola* more than those of any other extant, pinnate species. Additionally, having the carinae begin in the upper half of the stipes is unique to these two species. However, *A. rupicola* may not be the parent of all elements of *A. pentagona*. Some specimens of *A. pentagona* have

a tendency toward relatively larger and slightly more compound laminae and smaller ultimate divisions, suggesting an *A. parvisegmenta* parentage for these collections.

Adiantopsis rupicola is frequently spelled incorrectly as *A. rupincola*. Tryon and Tryon (1982) consistently use this incorrect spelling, and some specimens are determined with it. However, Maxon (1908) published the species as *A. rupicola*, and on subsequent determinations used that spelling. Therefore, *rupicola* does not appear to be an orthographic error and should be used.

Selected specimens examined. CUBA. **Pinar del Río**: Trail from Buenaventura to San Juan De Guacamalla, *P. Wilson 9349* (NY [2], US); Vedado, Habana, Las Pozas, N slopes of Pan de Guajaibon, *Bro. Alain 2416* (US); Valle del Ruisenor, near Vinales, *G. R. Proctor 16363* (GH [2]); Banos San Vicente, *N. L. Britton 7497, E. G. Britton, C. S. Gager* (NY, US); El Valle de Ancon, near San Vicente, *C. V. Morton 9791* (DUKE, US); Sierra Guacamayas, Mogoe de la Baliza, on mtn. top, *E. L. Ekman 17986* (US); Limestone hills between Rio Cuaguateje and the Sierra Guane, *J. A. Shafer 10453* (GH, NY, US); On limestone rock, N foot of Costanera de San Vicente, *Bro. Leon 14352* (NY).

9. Adiantopsis vincentii M. S. Barker & Hickey, sp. nov. TYPE: Cuba. Las Villas, Las Vegas de Mataguá, Trinidad Mtns., Feb. 22, 1956, *C. V. Morton 10819* (holotype, US!; isotype, DUKE!). Figure 10.

Laminae tripinnatae; axes marcescentes. Ab *A. parvisegmenta* segmentis ultimis fertilis planis, textura papyracea, ab *A. reesii* segmentis ultimis praebentibus apices integros, rhachidibus 0.6–1.2 mm diametro ad basim, et ab *A. rupicola* segmentis ultimis obovatis vel oblongis, laminis lanceatis vel lanceolatis, arcu e cellulis induratis 14 (modus) composito differt.

Rhizome erect to repent, to 2.7 cm long, 0.5–1.5 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, narrowly lanceate to acicular, basifixed, 2.60–5.68 mm long, 0.20–0.44 mm wide, bases truncate, margins entire to slightly repand, apices attenuate to cuneate. *Fronds* strict, 13.2–36.5 cm long. *Stipes* atropurpureous to atrocastaneous, always bicarinate adaxially, shorter than lamina, 2.9–13.8 cm long, 0.7–1.8 mm basal diam.; *carinae* beginning in basal ½ of stipe and continuing into rachis; *scales* extending 1.5–[2.13]–3.4 cm up the stipe, divergent, concolorous, tan, narrowly lanceate to acicular, pseudopeltate, 0.70–2.80 mm long, 0.06–0.46 mm wide, bases biauriculate to truncate, margins slightly repand to entire, apices attenuate; *hairs* septate-capitate. *Laminae* tripinnate, lanceate to lanceolate, drying green to brown, 12.2–28.5 cm long, 4.2–10.5 cm wide, apices difform, attenuate; *laminar tissue* papyraceous, hydathodes marginal; *hairs* with basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; *stoma* complanate, guard cells 40.75–53.79 μm long. *Laminar axes* marcescent with costae curling acroscopically, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *rachis* 0.6–1.2 mm basal diam.; *carinae* golden, grading into lamina; *scales* patent to appressed, linear, biseriate, 0.62–1.24 mm long, 0.02–0.04 mm wide, bases cuneate to truncate, apices attenuate. *Pinnae* ascending to patent, 23–32 pairs, alternate to sub-opposite, frequently incurved in basal half of lamina, straight distally, narrowly triangular to linear, slightly inequilateral, to 2.3–7.8 cm long, 0.7–1.8 cm wide, apices attenuate. *Pinnules* patent to slightly ascending, narrowly triangular to linear, basal pinnules 0.6–1.7 cm long, 0.3–1.0 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices cuneate to acute. *Ultimate divisions* patent to slightly ascending, articulate, obovate, oblong to elliptic, 2.7–6.0 mm long, 1.7–3.6 mm wide, bases cuneate, margins entire, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.1–0.5 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, obscure to occult. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.46–0.70 mm long, 0.40–0.50 mm wide, margin slightly erose to entire. *Sporangia* subglobose, long stalked, arcus of 12–16 indurated cells, these 32.60–52.16 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 32.60–44.01 μm diam., echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. *Adiantopsis vincentii* is a rare endemic in the Escambray Mountains of Cienfuegos, Sancti Spiritus, and Villa Clara Provinces, Cuba.

Notes. *Adiantopsis vincentii* is most likely to be confused with either *A. rupicola* or *A. parvisegmenta*. The generally smaller, obovate to oblong ultimate divisions and lanceate to lanceolate lamina of *A. vincentii* distinguish it from *A. rupicola*, which has generally larger ultimate divisions that are trullate to oblong and a narrowly triangular to lanceate lamina. *Adiantopsis vincentii* may be distinguished from *A. parvisegmenta* by three characters. The lamina of *A. vincentii* is papyraceous whereas the lamina of *A. parvisegmenta* is spongiose. *Adiantopsis vincentii* is tripinnate with a generally narrower lamina than the quadripinnate and broader lamina of *A. parvisegmenta*. Also, the fertile divisions of *A. vincentii* are

Figure 10. —A. *Adiantopsis vincentii* (*C. V. Morton 10389*, US). Scale bar = 3 cm. —B. Ultimate divisions of *A. vincentii*. Scale bar = 0.5 cm.

more or less flat, whereas the fertile divisions of *A. parvisegmenta* are strongly revolute.

Based on the sizes of guard cells, spores, and indurated arcus cells, *Adiantopsis vincentii* is placed with a putative diploid group of species. *Adiantopsis vincentii* is also the only hemi-dimorphic Caribbean *Adiantopsis*. On herbarium specimens with large rhizomes, and thus presumed to be mature plants, the fertility of the fronds is strongly correlated with frond size. The smallest fronds are consistently sterile, with a gradual increase in the number of sori and sporangia on progressively larger fronds. This pattern is not evident on specimens of other *Adiantopsis* taxa, and may serve as a useful character for recognizing the species if it can be confirmed to be unique.

Presently, *Adiantopsis vincentii* is not convincingly implicated in any patterns of reticulate evolution in *Adiantopsis*. However, it is possible that some elements of *A. pentagona* may have an *A. vincentii* parentage although no explicit hypothesis is presented. Future molecular studies should include *A. vincentii*, because the range of ultimate division variation in *A. pentagona* includes the character states that would likely be inherited from an *A. vincentii* parent.

Adiantopsis vincentii is named in honor of Michael A. Vincent, curator of the Willard Sherman Turrell Herbarium (MU) at Miami University, Oxford, Ohio. Dr. Vincent has continued to expand the collection at MU and has raised the Institution's standing in the world of botany through his activities as curator. Further, he has spent a significant amount of time dealing with research loans, and through these activities facilitates the research of many at Miami University.

Paratypes. CUBA. **Las Villas**: Trinidad Mtns., San Blas-Buenos Aires, *R. A. Howard 6542* (GH, MO, NY [2]); Trinidad Mtns., Buenos Aires, *C. V. Morton 10389* (US); Las Vegas de Matagua, Trinidad Mtns., *C. V. Morton 10544* (US). **Unknown Province**: Cuba, *Eggers 5399* (F).

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SUPPORT FOR AN EXPANDED *SOLMS-LAUBACHIA* (BRASSICACEAE): EVIDENCE FROM SEQUENCES OF CHLOROPLAST AND NUCLEAR GENES[1,2]

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Abstract

Sequences of the plastid maturase (*mat*K) and nuclear chalcone synthase (*Chs*) were analyzed separately and in combination to assess phylogenetic relationships of *Solms-laubachia* Muschl. (all nine known species and two undescribed ones) to the genera *Baimashania* Al-Shehbaz, *Parrya* R. Br., *Desideria* Pamp., *Leiospora* (C. A. Mey.) Dvořák, *Christolea* Cambess., and *Phaeonychium* O. E. Schulz (Brassicaceae). *Baimashania* is clustered with *Aubrieta deltoidea* (L.) DC. and *Arabis blepharophylla* Hook. & Arn. *Solms-laubachia*, *Desideria*, *Leiospora*, *Christolea*, and *Phaeonychium* are more closely related to *Matthiola* R. Br. than to *Parrya*, and they form a well-supported clade. Within this clade, *Leiospora* is sister to a subclade containing the sister groups *Christolea* and *Solms-laubachia* s.l. The *Solms laubachia* s.l. group contains *Solms-laubachia*, *Desideria*, and a species of *Phaeonychium*. Neither *Solms-laubachia* nor *Desideria* is monophyletic, whereas *Phaeonychium jafrii* Al-Shehbaz is embedded within the group. Therefore, our results suggest that *Solms-laubachia* be expanded to include *Desideria* and *P. jafrii*. Nevertheless, more species of *Desideria*, *Parrya*, and *Phaeonychium* are needed to further test our findings.

Key words: Brassicaceae, *Christolea*, *Chs*, *Desideria*, *Leiospora*, *mat*K, *Parrya*, *Phaeonychium*, phylogeny, *Solms-laubachia*.

The Brassicaceae (Cruciferae) consist of approximately 340 genera and 3350 species (Al-Shehbaz, 1984; Appel & Al-Shehbaz, 2003). They are a monophyletic family characterized by a number of synapomorphies, including flower structure (e.g., four sepals, four petals, often six tetradynamous stamens) and often a dehiscent capsule derived from a bicarpellate pistil with a septum dividing its ovary into two locules. Many plants of this family are common vegetables (e.g., cabbages, broccoli, cauliflower, Brussels sprouts, radishes, turnips, watercress). *Arabidopsis thaliana* (L.) Heynh., the model organism in plant experimental biology, belongs to the Brassicaceae.

Before the advent of molecular systematics, classification systems of the family (e.g., Hayek, 1911; Schulz, 1936; Janchen, 1942; Al-Shehbaz, 1984) were based almost exclusively on morphology. Over the past decade, molecular studies have greatly contributed to a better understanding of phylogenetic relationships within the Brassicaceae. Such studies show that many characters that have been commonly used to define tribal and subtribal divisions in the family are homoplasious. As a result, many tribes as traditionally recognized (e.g., Arabideae DC., Lepidieae DC., Euclidieae DC., Sisymbrieae DC.) are highly artificial (Koch et al., 2003; Al-Shehbaz et al., 2006). Generic limits within the family have also been a major source of controversy (Al-Shehbaz, 1984; Appel & Al-Shehbaz, 2003; Al-Shehbaz et al., 2006). However, molecular data have shed enormous light on the monophyly of various genera. For example, results from the nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS) sequence data show that *Arabis* L. and *Arabidopsis* Heynh., as traditionally delimited, are polyphyletic because they included purportedly unrelated species that had been assigned to many other genera (Koch et al., 1999; Al-Shehbaz et al., 1999; Al-Shehbaz, 2003; O'Kane & Al-Shehbaz, 2003; Al-

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Shehbaz, 2005). Warwick et al. (2002, 2004) have shown that generic limits of *Sisymbrium* L. and *Smelowskia* C. A. Mey. need reconsideration.

Another taxonomically difficult group involves several Himalayan and Central Asian genera, including *Solms-laubachia* Muschl. (9 spp.), *Desideria* Pamp. (12 spp.), *Leiospora* (C. A. Mey.) Dvořák (6 spp.), *Christolea* Cambess. (2 spp.), *Parrya* R. Br. (25 spp.), and *Phaeonychium* O. E. Schulz (7 spp.) (Appel & Al-Shehbaz, 2003). These genera occupy similar habitats (alpine scree slopes and limestone crevices) and exhibit overlapping morphological characters (e.g., perennial habit, latiseptate or terete fruits, well-defined basal rosettes, non-saccate sepals). Consequently, the same species have often been placed in different genera. For example, *Desideria pumila* (Kurz) Al-Shehbaz was originally described as *Parrya* (Kurz, 1872) and later transferred to *Christolea* (Jafri, 1955), *Vvedenskeyella* Botsch. (Botschantsev, 1955), or *Desideria* (Al-Shehbaz, 2001).

Parrya is most highly diversified in central Asia but has three species occurring in Arctic and subarctic Asia and North America (Appel & Al-Shehbaz, 2003). Four of the nine known species of *Solms-laubachia*, three of the 12 of *Desideria*, and all six of *Leiospora* were originally described as species of *Parrya* (Schulz, 1936). Recent morphological (Al-Shehbaz, 2001; Al-Shehbaz & Yang, 2001) and cytological (Yue et al., 2003, 2004) studies have indicated that while *Desideria*, *Solms-laubachia*, *Christolea*, and *Leiospora* are closely related to one another, together they are distinct from *Parrya*. Nevertheless, none of these genera have been included in phylogenetic analyses based on molecular data (Koch et al., 2003).

Baimashania Al-Shehbaz (2 spp.) is a recently described genus from China based on specimens that have been misidentified as species of *Solms-laubachia* or *Leiospora* (Al-Shehbaz, 2000b).

The objective of this study was to infer phylogenetic relationships of *Solms-laubachia* to the presumably related genera *Baimashania*, *Christolea*, *Desideria*, *Leiospora*, *Parrya*, and *Phaeonychium* based on sequences of the chloroplast gene *mat*K (maturase) and the nuclear gene *Chs* (chalcone synthase). These two markers have been used successfully in resolving generic relationships within Brassicaceae (e.g., Koch et al., 2000, 2001).

Materials and Methods

Plant Material

Fifty samples were used in this study, including 11 species of *Solms-laubachia* (nine in total plus two undescribed species), four of *Desideria* (of 12), two of *Leiospora* (of six), and one each of *Baimashania* (of two), *Phaeonychium* (of seven), *Christolea* (of two), and *Parrya* (of 25). The remaining samples represent 24 genera of Brassicaceae. This broad sampling of the family is necessary because none of these genera mentioned above have been included in previous phylogenetic analyses and it is unclear whether they form a clade and what taxa are their outgroups. As in Koch et al. (2001), we used *Aethionema grandiflorum* Boiss. & Hohen. as the outgroup because *Aethionema* R. Br. is sister to the rest of Brassicaceae (Zunk et al., 1996; Galloway et al., 1998). In their recently proposed tribal classification of the family, Al-Shehbaz et al. (2006) placed *Parrya* with *Matthiola* R. Br. in the tribe Anchonieae DC., *Baimashania* in the Arabideae, and *Solms-laubachia*, *Desideria*, and *Leiospora* in the Euclidieae.

DNA Extraction, PCR, and Sequencing

Total genomic DNAs were extracted from silica gel–dried leaves using a Qiagen DNeasy Plant Mini Kit following the manufacturer's protocol (Santa Clarita, California). Genomic DNAs of three accessions of *Desideria* and one each of *Leiospora* and *Solms-laubachia* were kindly provided by Jason R. Grant (Université de Neuchâtel, Switzerland).

*Plastid mat*K

Double-stranded DNAs of *mat*K were amplified using primers *trn*K-710F* and *trn*K-2R* originally designed by Johnson and Soltis (1994) and slightly modified later by Koch et al. (2001). A 50-μL polymerase chain reaction (PCR) included 50–100 ng DNA, 5 μL of 10× *Taq* polymerase buffer, 4 μL of dNTP (2.5 mM), 4 μL of $MgCl_2$ (25 mM), 2 μL of each primer (10 μM), 0.5 μL of *Taq* polymerase (5 units/μL), and 29.5–31.5 μL of sterilized water, depending on the amount of DNA used. The PCR profile used to amplify the *mat*K region included 34 cycles (94°C for 1 minute 30 seconds, 48–52 C for 2 minutes, 72°C for 3 minutes) and a final extension at 72°C for 15 min. PCR products were gel-purified using a Qiagen Gel Purification Kit, following the manufacturer's protocol. Both strands were sequenced using the ABI BigDye Florescent Terminator Chemistry (Applied Biosystems, Foster City, California) and the following primers: *trn*K-710F*, *trn*K-2R*, *mat*K-1F, *mat*K-312F, *mat*K-495F, *mat*K-495R, *mat*K-1089R, and *mat*K-1089R (Koch et al., 2001).

Nuclear Chs

PCR amplification of the entire gene, including the promoter region, was performed using the primers

Chs-For1 and *Chs*-Rev 5 (Koch et al., 1999). Components of the PCR reaction were the same as those described for the *mat*K gene, and the PCR program included a 5-minute denaturation at 95°C and 35 cycles, followed by an additional 15-minute extension at 72°C. Each cycle consisted of 1 minute of denaturing at 95°C, 1 minute of annealing at 55°C, and a 2-minute extension at 72°C. All of the PCR amplifications resulted in a single predominant band on an agarose gel. PCR products were gel-purified using a Qiagen Gel Purification Kit, following the manufacturer's protocol, and then were cloned into the pGEM-T cloning vector (Promega, Madison, Wisconsin). To detect possible allelic variation, two clones from two independent PCR reactions were sequenced respectively for each sample. Sequencing primers included vector primers T7 and Sp6, and Koch et al.'s (1999) primers (*Chs*-FOR2, *Chs*-REV2, *Chs*-REV3, *Chs*-FOR4, and *Chs*-REV4).

Sequences were analyzed using an Automated ABI Genetic Analyzer 3100, and were then edited using Sequencher (version 4.0, Gene Codes Corp., Inc., Ann Arbor, Michigan). The edited sequences were then aligned manually.

PHYLOGENETIC ANALYSES

Phylogenetic analyses were performed for the data sets individually and in combination using maximum parsimony (Farris et al., 1970; Fitch, 1971) and Bayesian methods (Rannala & Yang, 1996). The heuristic searches for maximum parsimony analysis were conducted using PAUP*4.0 (Swofford, 2002) with the following conditions: random sequence addition with 1000 replicates and 10 trees held at each step, tree bisection-reconnection branch swapping, and MULPARS on and the steepest descent off. Character state changes were unordered and equally weighted in the analysis, and gaps were treated as missing data. Bootstrap analyses of 1000 replicates were performed to estimate the support for individual clades using heuristic tree search options as in the maximum parsimony analyses. To further assess relative support for the individual clades, a decay analysis (Sorenson, 1996) was also used. The best evolutionary model of DNA substitutions for the Bayesian analysis was determined using Modeltest version 3.06 (Posada & Crandall, 1998). Bayesian analyses (Rannala & Yang, 1996; Mau et al., 1999) were carried out using MrBayes version 3.0b3 (Huelsenbeck & Ronquist, 2001, available at <http://mrbayes.csit.fsu.edu>) with the model parameters as estimated in Modeltest. Bayesian analysis was started from random trees and employed four Markov chain Monte Carlo runs, monitored over 2×10^6 generations, sampling trees every 100 generations. Runs were repeated twice to confirm results. The resulting log likelihood and number of generations were plotted to determine the point after which the log likelihoods had stabilized. After discarding the trees saved prior to this point as burn-in, the remaining trees were imported into PAUP*, and a 50% majority-rule tree was produced to obtain posterior probabilities of the clades (Huelsenbeck & Ronquist, 2001). Internodes with posterior probabilities ≥ 95% were considered statistically significant.

The incongruence length difference (ILD) test (Farris et al., 1994, as implemented in PAUP*) was used to assess potential conflicts between the phylogenetic signals from the two different DNA fragments. For the test, 100 replicates were analyzed with a heuristic search, each with 10 random sequence addition replicates. In addition, we compared *mat*K and *Chs* trees to examine whether there were well-supported (> 70% bootstrap support), but conflicting clades.

RESULTS

SEQUENCE CHARACTERISTICS

Twenty-five *mat*K and 24 *Chs* sequences were newly gathered in this study. An additional 26 *mat*K and *Chs* sequences were obtained from GenBank and included in this study (Table 1).

The amplified segment also included a 300-bp fragment at the 3′ end of the *trn*K region. However, the alignment of this region across Brassicaceae was ambiguous, and thus our analyses did not include sequences of the segment. The sequences of the *mat*K gene were aligned readily by hand, resulting in a data set of 1536 bp, of which 530 sites were variable and 237 sites (15.43%) were potentially parsimony informative. The sequence divergence ranged from 6.02%–8.27% between the outgroup and ingroup and from 0.067%–7.93% within the ingroup.

Limits of the introns and promoter regions of the *Chs* gene were determined by comparison with published sequences (Koch et al., 1999). These regions could not be aligned unambiguously across Brassicaceae and thus were removed from phylogenetic analyses. However, exon sequences were aligned readily by hand, and the alignment resulted in a data set of 1174 bp, of which 511 were variable sites and 364 sites (31%) were potentially parsimony informative. The sequence divergence ranged from 19.3%–23.6% between the outgroup and ingroup and from 0.34%–17.9% within the ingroup.

Results of the ILD test showed that our *mat*K and *Chs* data sets were not significantly different (P =

Table 1. Vouchers and sources of species used in this study. An asterisk (*) indicates that sequences were obtained from GenBank.

Taxon	Voucher	Source	*mat*K	*Chs*
Aethionema grandiflorum Boiss. & Hohen.			AF144354*	AF112082*
Alliaria petiolata (M. Beib.) Cavara & Grande			AF144363*	AF144537*
Arabidopsis thaliana (L.) Heynh.			AF144348*	AF112086*
Arabis blepharophylla Hook. & Arn.			AF144353*	AF112087*
Arabis divaricarpa A. Nelson			AF144351*	AF112090*
Aubrieta deltoidea (L.) DC.			AF144352*	AF112109*
Baimashania pulvinata Al-Shehbaz	*Yue 0222 (KUN)*	China, Yunnan, Deqing	DQ409251	DQ409227
Barbarea vulgaris R. Rr.			AF144330*	AF112108*
Capsella rubella Reuter			AF144334*	AF112106*
Cardamine amara L.			AF144337*	AF112085*
Cardamine penzesii Ančev & Marhold			AF144364*	AF144538*
Cardamine rivularis Schur			AF144365*	AF144539*
Christolea crassifolia Cambess.	*B. Bartholomew et al. 9499* (MO)	China, Xinjiang	DQ409256	DQ409232
Cochlearia danica L.			AF174531*	AF144532*
Crucihimalaya himalaica (Edgew.) Al-Shehbaz, O'Kane & R. A. Price			AF144356*	AF144531*
Desideria baiogoinensis (K. C. Kuan & Z. X. An) Al-Shehbaz	*Yue 0246* (KUN)	China, Tibet, Mozhugongka	DQ409252	DQ409228
Desideria himalayensis (Cambess) Al-Shehbaz	*McBenth 1486* (E)	Nepal	DQ409266	DQ409242
Desideria linearis (N. Busch) Al-Shehbaz	*B. Bartholomew et al. 9549* (MO)	China, Xinjiang	DQ409254	DQ409230
Desideria stewartii (Anderson) Al-Shehbaz	*McBeath 2105* (E)	India	DQ409265	DQ409241
Erysimum handel-mazzettii Polatschek	*Yue 0369* (KUN)	China, Yunnan, Zhongdian	DQ409262	DQ409238
Fourraea alpina (L.) Greuter & Burdet			AF144335*	AF112102*
Halimolobus perplexa (Henderson) Rollins var. *perplexa*			AF144346*	AF112094*
Ionopsidium abulense (Pau.) Rothm.			AF144368*	AF144542*
Leiospora exscapa (C. A. Mey.) Dvořák	*Murray et al. 457* (ALA)	Russia	DQ409263	DQ409239
Leiospora pamirica (Botsch. & Vved.) Botsch. & Pachom.	*B. Bartholomew et al. 9790* (MO)	China, Xinjiang	DQ409255	DQ409231
Lepidium campestre (L.) R. Br.			AF144359*	AF144534*
Matthiola incana (L.) R. Br.			AF144361*	AJ427536*
Microthlaspi perfoliatum (L.) F. K. Meyer			AF144362*	AF144536*
Olimarabidopsis cabulica (Hook. f. & Thompson) Al-Shehbaz, O'Kane & R. A. Price			AF144358*	AF144533*
Olimarabidopsis pumila (Stephan) Al-Shehbaz, O'Kane & R. A. Price			AF144345*	AF112092*
Parrya nudicaulis (L.) Regel	*Yue 0244* (KUN)	China, Tibet, Lhasa	DQ409253	DQ409229
Phaeonychium jafrii Al-Shehbaz	*Yue 0233* (KUN)	China, Tibet, Lhasa	DQ409261	DQ409237
Rorippa amphibia (L.) Besser			AF174530*	AF144530*
Sinapis alba L.			X04826*	X16437*
Sisymbrium irio L.			AF144366*	AF144541*
Solms-laubachia eurycarpa (Maxim.) Botsch., 1	*SAB Yushu Exped. 2178* (E)	China, Qinghai, Yushu	DQ409264	DQ409240
Solms-laubachia eurycarpa (Maxim.) Botsch., 2	*Yue 0158* (KUN)	China, Yunnan, Deqing	DQ409243	DQ409219
Solms-laubachia lanata Botsch.	*Yue 0234* (KUN)	China, Tibet, Lhasa	DQ409246	DQ409222
Solms-laubachia linearifolia (W. W. Sm.) O. E. Schulz	*Yue 0157* (KUN)	China, Yunnan, Deqing	DQ409249	DQ409225
Solms-laubachia minor Hand.-Mazz.	*Yue 0379* (KUN)	China, Sichuan, Yanyuan	DQ409257	DQ409233

Table 1. Continued.

Taxon	Voucher	Source	*mat*K	*Chs*
Solms-laubachia platycarpa (Hook. f. & Thomson) Botsch.	*Yue 0238* (KUN)	China, Tibet, Dangxion	DQ409245	DQ409221
Solms-laubachia pulcherrima Muschl.	*Yue 0153* (KUN)	China, Yunnan, Lijian	DQ409247	DQ409223
Solms-laubachia retropilosa Botsch.	*Yue 0248* (KUN)	China, Sichuan, Kangding	DQ409248	DQ409224
Solms-laubachia sp. indet. 1	*D. E. Boufford et al. 30727* (HUH)	China, Sichuan, Xiangcheng	DQ409258	DQ409234
Solms-laubachia sp. indet. 2	*D. E. Boufford et al. 31975* (HUH)	China, Tibet, Riwoqe	DQ409260	DQ409236
Solms-laubachia xerophyta (W. W. Sm.) Comber, 1	*Yue 0250* (KUN)	China, Sichuan, Daocheng	DQ409244	DQ409220
Solms-laubachia xerophyta (W. W. Sm.) Comber, 2	*Yue 0251* (KUN)	China, Yunnan, Zhongdian	DQ409259	DQ409235
Solms-laubachia zhongdianensis J. P. Yue, Al-Shehbaz & H. Sun	*Yue 0156* (KUN)	China, Yunnan, Zhongdian	DQ409250	DQ409226
Thlaspi arvense L.			AF144360*	AF144535*
Turritis glabra L.			AF144333*	AF112091*

0.51). Furthermore, maximum parsimony and Bayesian analyses based on the two individual data sets resulted in several well-supported monophyletic groups, and there were no well-supported (bootstrap support > 70% and posterior probability > 95%) but incongruent clades (trees not shown). Therefore, results of phylogenetic analyses based on the combined data set are presented below.

PHYLOGENETIC RELATIONSHIPS

The combined data set of *mat*K and *Chs* had 50 taxa and 2710 sites, of which 1669 (61.6%) were invariable, 440 (16.2%) were unique nucleotide changes, and 601 (22.2%) were parsimony informative. The sequence divergence ranged from 6.02%–8.27% between the outgroup and ingroup and 0.067%–7.93% within the ingroup.

Parsimony analyses yielded six trees of 2889 steps; the strict consensus is shown in Figure 1 (consistency index (CI) = 0.50, retention index (RI) = 0.69, and rescaled consistency index (RC) = 0.35). The relationships of the taxa whose *mat*K and *Chs* sequences were obtained from the GenBank (cf. Table 1) were consistent with those of Koch et al. (2001). To these, we included our samples of *Baimashania pulvinata* Al-Shehbaz and *Erysimum handel-mazzettii* Polatschek. The former species clustered with *Aubrieta deltoidea* (L.) DC. and *Arabis blepharophylla* Hook. & Arn. (Clade A) and was remotely related to both *Solms-laubachia* and *Leiospora*, whereas the latter was positioned in a clade including *Arabidopsis*, *Turrits* L., *Olimarabidopsis* Al-Shehbaz, O'Kane & R. A. Price, *Capsella* Medik., *Arabis* L., *Halimolobus* Tausch, and *Crucihimalaya* Al-Shehbaz, O'Kane & R. A. Price.

Parrya nudicaulis (L.) Regel was strongly supported as sister to the clade (Clade B, Fig. 1) containing *Matthiola incana* (L.) R. Br., *Leiospora*, *Christolea*, *Solms-laubachia*, *Desideria*, and *Phaeonychium jafrii* Al-Shehbaz. *Matthiola* was sister to the clade containing the latter five genera (Clade C, Fig. 1). In Clade C, two accessions of *Leiospora* formed a well-supported group, occupying a sister position to other remaining taxa that formed Clade D (Fig. 1). Species of *Solms-laubachia*, *Desideria*, and *P. jafrii* formed a clade (Fig. 1, Clade E), with *C. crassifolia* Cambess. as a sister group. Within Clade E, there were three subclades, the first of which (Clade F) included *D. linearis* (N. Busch) Al-Shehbaz, *D. stewartii* (Anderson) Al-Shehbaz, and *D. himalayensis* (Cambess.) Al-Shehbaz. The second had *P. jafrii* alone and was sister to the third clade (Clade G), which contained *D. baiogoinensis* (K. C. Kuan & Z. X. An) Al-Shehbaz and all species of *Solms-laubachia*. While interspecific relationships of *Solms-laubachia* were weakly or moderately supported, *S. lanata* Botsch. and *D. baiogoinensis* clustered together with strong support (bootstrap = 94%). Clade G was a trichotomy including *D. baiogoinensis* + *S. lanata*, *S. platycarpa* (Hook. f. & Thomson) Botsch., and Clade H. Within this clade, *S. retropilosa* Botsch. and *S. linearifolia* (W. W. Sm.) O. E. Schulz formed a moderately supported clade (bootstrap = 74%) that was sister to

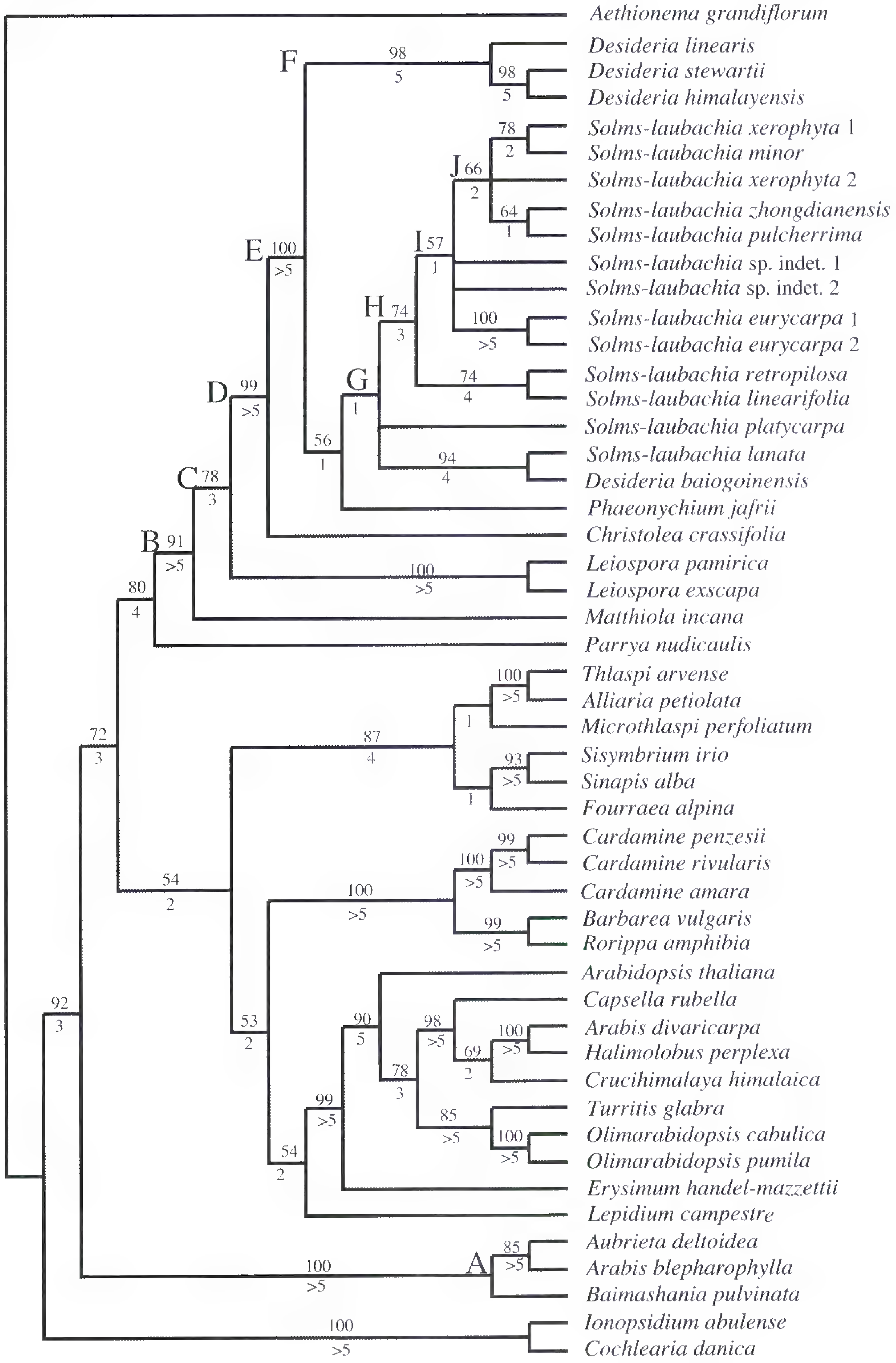

Figure 1. Strict consensus of six parsimonious trees based on the combined data set of *mat*K and *Chs* genes. Numbers above and below branches are bootstrap percentages and decay indices, respectively. Letters A–J refer to clades discussed in the text.

a polytomous branch (Clade I, bootstrap = 57%). Clade I contained *S. eurycarpa* (Maxim.) Botsch., two undescribed species (*Solms-laubachia* sp. indet. 1 and 2), and Clade J, which consists of *S. minor* Hand.-Mazz. + one accession of *S. xerophyta* (W. W. Sm.) Comber (bootstrap = 78%), *S. zhongdianensis* J. P. Yue, Al-Shehbaz & H. Sun + *S. pulcherrima* Muschl. (bootstrap = 64%), and the second accession of *S. xerophyta* (W. W. Sm.) Comber.

The best-fit model of evolution for the combined *mat*K and *Chs* data set was GTR + I + G, as indicated by the Modeltest. The base frequencies were A = 0.287, C = 0.195, G = 0.19, T = 0.328, and the gamma distribution shape parameter was 0.6244. Bayesian analyses with the estimated parameters produced trees with identical topology to Figure 1, with a few discrepancies in the clade containing species of *Solms-laubachia*, *Desideria baiogoinensis*, and *Phaeonychium jafrii* (Fig. 2). *Phaeonychium jafrii* formed a sister relationship with Clade G in the maximum parsimony tree (Fig. 1), while in the Bayesian tree *S. platycarpa* was sister to the clade consisting of *D. baiogoinensis*, *P. jafrii*, and the remaining species of *Solms-laubachia* (Fig. 2). In the maximum parsimony tree, *S. eurycarpa* and the two undescribed *Solms-laubachia* species formed a polytomy. However, in the Bayesian tree, one undescribed species (*Solms-laubachia* sp. indet. 1) clustered with the two accessions of *S. eurycarpa*, while the other (*Solms-laubachia* sp. indet. 2) was sister to the clade containing *S. eurycarpa*, *S.* sp. indet. 1, *S. xerophyta*, *S. minor*, *S. zhongdianensis*, and *S. pulcherrima*. Nevertheless, the topological differences between the maximum parsimony and Bayesian trees were weakly supported.

Discussion

Schulz (1936) placed *Solms-laubachia* and *Parrya* (including *Leiospora*) with *Matthiola* in the tribe Matthioleae O. E. Schulz, *Christolea* in the tribe Sisymbrieae, and *Desideria* (as a synonym of *Ermania* Cham.) and *Phaeonychium* in the tribe Arabideae. These tribes were defined largely on the basis of silique fruits with incumbent cotyledons and open calyx (Sisymbrieae), accumbent cotyledons and closed calyx (Matthioleae), or accumbent cotyledon and open calyx (Arabideae). However, in the *mat*K + *Chs* tree (Fig. 1), *Matthiola* is sister to the clade containing *Christolea*, *Desideria*, *Solms-laubachia*, *Phaeonychium*, and *Leiospora* (bootstrap = 78%), suggesting that these genera are closely related to one another and, together, to *Matthiola*. Our results provide further evidence that most tribes of Schulz (1936) are not monophyletic (Koch et al., 2003; Al-Shehbaz et al., 2006).

Specimens of *Baimashania pulvinata*, a species endemic to northwestern Yunnan, had been misidentified as *Solms-laubachia ciliaris* (Bureau & Franch.) Botsch. (Al-Shehbaz, 2000b). Our sequence data did not place *Baimashania* close to *Solms-laubachia*. Instead, these data support a close relationship of *Baimashania* with *Aubrieta* Adans. and *Arabis*. Therefore, our results support the recognition of *Baimashania* as a separate genus from *Solms-laubachia*, and Al-Shehbaz et al. (2006) assigned these two genera to the tribes Arabideae and Euclidieae, respectively.

In both the maximum parsimony and Bayesian trees (Figs. 1, 2), *Parrya* is sister to the clade (B) containing *Matthiola*, *Leiospora*, *Christolea*, *Desideria*, *Solms-laubachia*, and *Phaeonychium*, indicating that none of the latter five genera is closely related to *Parrya*. This is supported by morphological and cytological evidence (Al-Shehbaz, 2001; Al-Shehbaz & Yang, 2001; Yue et al., 2003, 2004). *Solms-laubachia* differs from *Parrya* in that it has wingless seeds, rounded replum concealed by the strongly angled valve margins, valves apically united with obsolete style and replum, fruits readily detached basally from the pedicel, entire stigmas or with non-decurrent lobes, and eglandular papillae. By contrast, *Parrya* has winged seeds, strongly flattened and readily visible replum, flat and not angled valve margins, valves readily separated from the well-developed styles, fruits persistently united basally with pedicels, stigmas with decurrent and connate lobes, and often glandular papillae (Al-Shehbaz & Yang, 2001). *Solms-laubachia*, *Desideria*, and *Christolea* are more similar to one another in chromosome morphology than they are to *Parrya* (Yue et al., 2003, 2004). Nevertheless, an extensive sampling of *Parrya* is needed to further test the phylogenetic position of the genus.

Solms-laubachia, *Desideria*, and *Phaeonychium jafrii* form a well-supported clade (E, Figs. 1, 2), and their close relationship is supported by the smooth fruit valve (Al-Shehbaz, 2000a, 2001). Together, these three genera form a clade sister to *Christolea*. Several morphological synapomorphies offer support for the relationship, such as the presence of cauline leaves, equal and non-saccate sepals, obsolete or distinct style, non-decurrent stigma lobes, and wingless seeds. By contrast, in *Leiospora*, which is sister to the clade of *Christolea*, *Solms-laubachia*, *Desideria*, and *Phaeonychium jafrii*, cauline leaves are absent, sepals unequal and saccate, style absent, stigma lobes strongly decurrent, and seeds winged (Al-Shehbaz, 2000a, 2001).

Species of *Desideria* form a clade (F, Figs. 1, 2) except for *D. baiogoinensis*, which is embedded with-

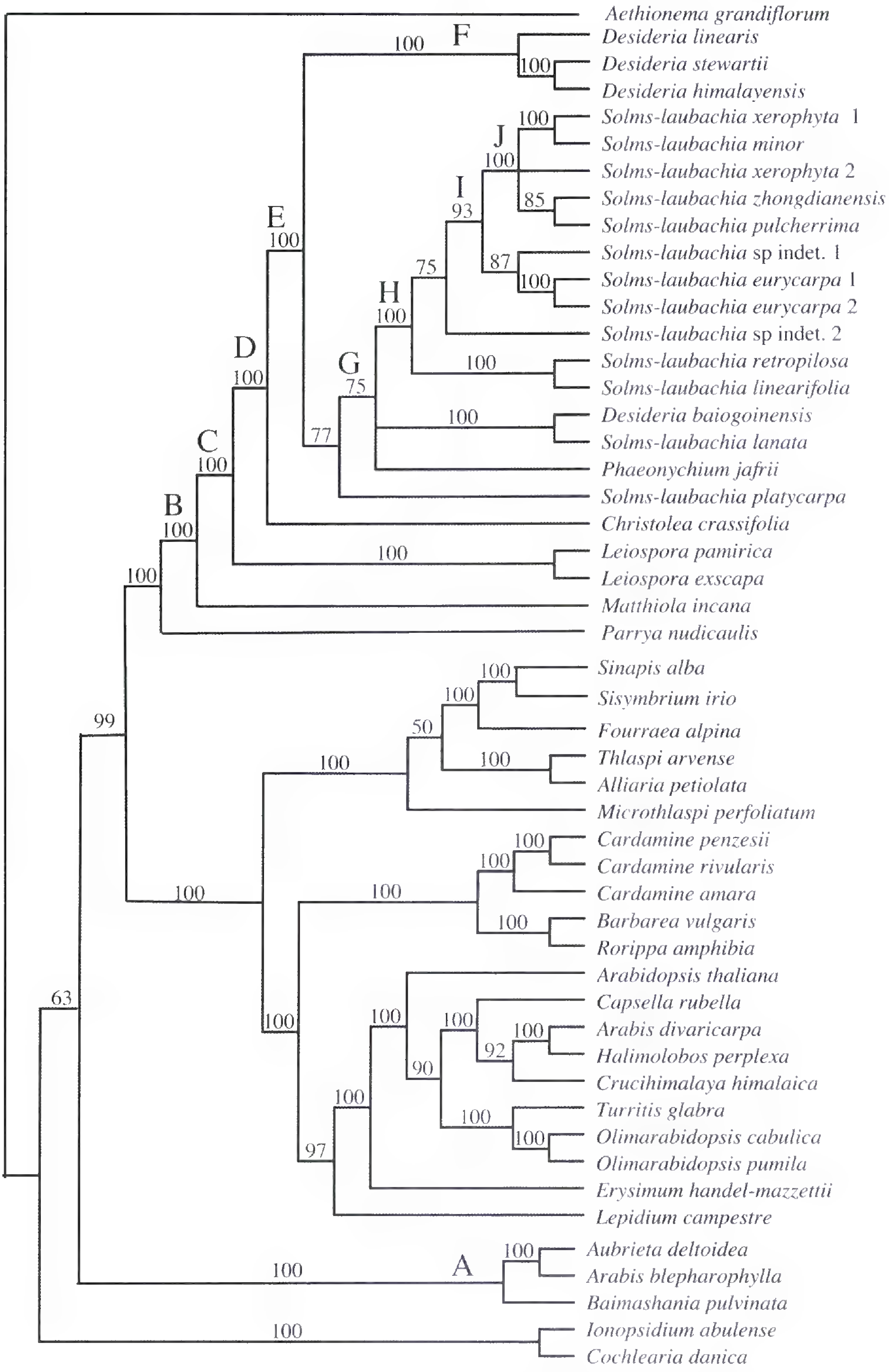

Figure 2. Majority consensus tree inferred from Bayesian analyses of the combined data set of *mat*K and *Chs* genes. Numbers at branches are posterior probabilities, and letters A–J refer to clades discussed in the text.

in *Solms-laubachia*, suggesting that *Desideria* may be polyphyletic and *Solms-laubachia* paraphyletic. *Phaeonychium jafrii* is either sister to a weakly supported clade (G, Fig. 1) containing *Solms-laubachia* and *D. baiogoinensis* or is embedded within *Solms-laubachia* (G, Fig. 2). Therefore, our results support an expanded *Solms-laubachia*, i.e., *Solms-laubachia* s.l., including species of *Desideria* and *P.*

jafrii as well. However, *Phaeonychium* is a heterogeneous genus of seven species distributed in central Asia and centered in southwestern China (Al-Shehbaz, 2000a; Zhou et al., 2001). More species are needed to further test the phylogenetic relationships of *Phaeonychium* before a proposal can be made to merge it with *Solms-laubachia* and *Desideria*. Nevertheless, sequences of *mat*K and *Chs* suggest the union of *Solms-laubachia* and *Desideria*.

Within *Solms-laubachia*, *S. retropilosa* and *S. linearifolia* are closely related (bootstrap = 74%, Fig. 1, and posterior probability = 100%, Fig. 2). *Solms-laubachia minor*, *S. pulcherrima*, *S. zhongdianensis*, and two accessions of *S. xerophyta* form a clade (bootstrap = 66%, Fig. 1, and posterior probability = 100%, Fig. 2). However, two accessions of *S. xerophyta* do not cluster together, with one (*Yue 0250*) from Sichuan and the other (*Yue 0251*) from Yunnan. Further morphological studies are needed to determine whether they might represent different species. Given the low phylogenetic resolution from *matK* and *Chs* data for interspecific relationships of *Solms-laubachia* s.l., further studies with additional data from more rapidly evolving DNA regions are warranted.

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REVISIÓN DEL GÉNERO *ACAENA* (ROSACEAE) EN CHILE[1]

Alicia Marticorena[2]

Resumen

Se realizó una revisión taxonómica del género *Acaena* en Chile, utilizando caracteres morfológicos clásicos. Se reconocen veinte especies para Chile continental y Archipiélago de Juan Fernández, las que se ubican en seis secciones. Los caracteres de mayor utilidad para reconocer las especies son el tipo de inflorescencia, forma de los folíolos, así como la forma y ornamentación de la cupela. Las siguientes especies son lectotipificadas: *A. alpina* Poepp. ex Walp., *A. caespitosa* Gillies ex Hook. et Arn., *A. integerrima* Gillies ex Hook. et Arn., *A. macrocephala* Poepp., *A. magellanica* (Lam.) Vahl, *A. pinnatifida* Ruiz et Pav., *A. platyacantha* Speg., *A. splendens* Hook. et Arn. y *A. tenera* Alboff. Las siguientes especies fueron neotipificadas: *A. lucida* (Aiton) Vahl, *A. sericea* J. Jacq. y *A. trifida* Ruiz et Pav. var. *glabrescens* Regel et Körn. Los siguientes sinónimos fueron lectotipificados: *A. argentea* Ruiz et Pav. var. *breviscapa* Bitter, *A. argentea* Ruiz et Pav. var. *coriacea* Bitter, *A. argentea* Ruiz et Pav. var. *interrupte-pinnata* Bitter, *A. argentea* Ruiz et Pav. var. *lanigera* Bitter, *A. argentea* Ruiz et Pav. var. *subcalvescens* Bitter, *A. cadilla* Hook. f., *A. canescens* Phil., *A. cuneata* Hook. et Arn., *A. digitata* Phil., *A. digitata* Phil. var. *latifoliolata* Bitter, *A. digitata* Phil. var. *subpinnata* Bitter, *A. euacantha* Phil., *A. fuegina* Phil., *A. glandulifera* Bitter, *A. grandistipula* Bitter, *A. hirsuta* Phil., *A. ischnostemon* Bitter, *A. krausei* Phil., *A. krausei* Phil. subvar. *glabratula* Bitter, *A. longiaristata* H. Ross [= *A. magellanica* (Lam.) Vahl], *A. lucida* var. *villosula* Bitter, *A. macrostemon* Hook. f. subsp. *longiaristata* (H. Ross) Bitter var. *basipilosa* Bitter, *A. macrostemon* Hook. f., *A. magellanica* (Lam.) Vahl subsp. *pygmaea* Bitter, *A. magellanica* (Lam.) Vahl var. *glabrescens* Bitter, *A. microcephala* Schltdl., *A. multifida* Hook. f. subsp. *intercedens* Bitter, *A. neglecta* Bitter, *A. petiolulata* Phil., *A. pinnatifida* Ruiz et Pav. subsp. *hypoleuca* Bitter, *A. pinnatifida* Ruiz et Pav. subsp. *nudiscapa* Bitter, *A. pinnatifida* Ruiz et Pav. var. *uspallatensis* Bitter, *A. quinquefida* Phil., *A. splendens* Hook. et Arn. var. *brachyphylla* Bitter, *A. splendens* Hook. et Arn. var. *brevisericea* Bitter, *A. tenuipila* Bitter, *A. trifida* Ruiz et Pav. var. *argentella* Bitter, *A. trifida* Ruiz et Pav. var. *brachyphylla* Bitter, *A. trifida* Ruiz et Pav. var. *mollissima* Bitter y *A. renulosa* Griseb. Los siguientes sinónimos fueron neotipificados: *A. calcitrapa* Phil., *A. closiana* Gay, *A. hirta* Citerne y *A. macrostemon* Hook. f. subsp. *closiana* (Gay) Bitter.

Abstract

A taxonomic revision of the genus *Acaena* in Chile was carried out, using morphological characters. Twenty species belonging to six sections are recognized for continental Chile and Juan Fernandez Archipelago. The most useful characters for recognizing species are inflorescence type, the form of leaflets, as well as the form and ornamentation of the fruit. The following species are lectotypified: *A. alpina* Poepp. ex Walp., *A. caespitosa* Gillies ex Hook. et Arn., *A. integerrima* Gillies ex Hook. et Arn., *A. macrocephala* Poepp., *A. magellanica* (Lam.) Vahl, *A. pinnatifida* Ruiz et Pav., *A. platyacantha* Speg., *A. splendens* Hook. et Arn., and *A. tenera* Alboff. The following species were neotypified: *A. lucida* (Aiton) Vahl, *A. sericea* J. Jacq., and *A. trifida* Ruiz et Pav. var. *glabrescens* Regel et Körn. The following synonyms were lectotypified: *A. argentea* Ruiz et Pav. var. *breviscapa* Bitter, *A. argentea* Ruiz et Pav. var. *coriacea* Bitter, *A. argentea* Ruiz et Pav. var. *interrupte-pinnata* Bitter, *A. argentea* Ruiz et Pav. var. *lanigera* Bitter, *A. argentea* Ruiz et Pav. var. *subcalvescens* Bitter, *A. cadilla* Hook. f., *A. canescens* Phil., *A. cuneata* Hook. et Arn., *A. digitata* Phil., *A. digitata* Phil. var. *latifoliolata* Bitter, *A. digitata* Phil. var. *subpinnata* Bitter, *A. euacantha* Phil., *A. fuegina* Phil., *A. glandulifera* Bitter, *A. grandistipula* Bitter, *A. hirsuta* Phil., *A. ischnostemon* Bitter, *A. krausei* Phil., *A. krausei* Phil. subvar. *glabratula* Bitter, *A. longiaristata* H. Ross [= *A. magellanica* (Lam.) Vahl], *A. lucida* var. *villosula* Bitter, *A. macrostemon* Hook. f. subsp. *longiaristata* (H. Ross) Bitter var. *basipilosa* Bitter, *A. macrostemon* Hook. f., *A. magellanica* (Lam.) Vahl subsp. *pygmaea* Bitter, *A. magellanica* (Lam.) Vahl var. *glabrescens* Bitter, *A. microcephala* Schltdl., *A. multifida* Hook. f. subsp. *intercedens* Bitter, *A. neglecta* Bitter, *A. petiolulata* Phil., *A. pinnatifida* Ruiz et Pav. subsp. *hypoleuca* Bitter, *A. pinnatifida* Ruiz et Pav. subsp. *nudiscapa* Bitter, *A. pinnatifida* Ruiz et Pav. var. *uspallatensis* Bitter, *A. quinquefida* Phil., *A. trifida* Ruiz et Pav. var. *quinquefida* (Phil.) Reiche, *A. splendens* Hook. et Arn. var. *brachyphylla* Bitter, *A. splendens* Hook. et Arn. var. *brevisericea* Bitter, *A. tenuipila* Bitter, *A. trifida* Ruiz et Pav. var. *argentella* Bitter, *A. trifida* Ruiz et Pav. var. *brachyphylla* Bitter, *A. trifida* Ruiz et Pav. var. *mollissima* Bitter, and *A. renulosa* Griseb. The following synonyms were neotypified: *A. calcitrapa* Phil., *A. closiana* Gay, *A. hirta* Citerne, and *A. macrostemon* Hook. f. subsp. *closiana* (Gay) Bitter.

Key words: *Acaena*, Chile, Rosaceae, taxonomy.

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La familia Rosaceae Adans. posee cerca de 3000 especies distribuidas en alrededor de 100 géneros (Kalkman, 1988; Mabberley, 1997) los que corresponden a plantas leñosas y herbáceas, principalmente de regiones templadas y subtropicales del hemisferio norte (Cronquist, 1981; Heywood, 1985; Hutchinson, 1964–1967). Se caracteriza por presentar hojas alternas, raramente opuestas, simples, compuestas o disectas, en general acompañadas de un par de estípulas (Heywood, 1985). Las flores son solitarias o a menudo dispuestas en inflorescencias, en general son actinomorfas, hermafroditas, con un hipantio notorio (Cronquist, 1981; Mabberley, 1997).

Respecto de la polinización, las flores de las Rosáceas son poco especializadas, produciendo gran cantidad de polen, el que atrae a una amplia variedad de insectos grandes y pequeños (Jude et al., 1999). Sin embargo, géneros como *Acaena* Mutis ex L. y *Poterium* L., poseen flores muy reducidas, en parte unisexuales, sin pétalos ni néctar, y polinizadas por el viento (Heywood, 1985). En contraste con este carácter está la gran diversidad de frutos, tales como: aquenio, poliaquenio, drupa, polidrupa, cápsula, pomo, folículo, entre los más comunes (Spjut, 1994), los que entregan importantes características para diferenciarla en subfamilias (Heywood, 1985).

En Chile, la familia está formada por 15 géneros y 51 especies (Marticorena, 1991). La mayoría de las especies del género *Acaena* (aproximadamente 43), se distribuyen en el hemisferio sur, encontrándose también algunos representantes en el hemisferio norte como por ejemplo en México, California y Hawaii (Hutchinson, 1964–1967). El género pertenece a la tribu Poterieae Dumort. (Sanguisorbeae DC.) de la subfamilia Rosoideae Arn., y se encuentra relacionado morfológicamente a *Sanguisorba* L., *Poterium*, ambos de zonas templadas del hemisferio norte, y a *Margyricarpus* Ruiz et Pav., *Polylepis* Ruiz et Pav. y *Tetraglochin* Kunze ex Poepp., del hemisferio sur, todos ellos pertenecientes a la misma tribu, los comparten algunos caracteres tales como el tipo de fruto rodeado por el tubo del cáliz persistente, que puede presentar ornamentaciones y en las flores simples, dispuestas en cabezuelas o espigas (Hutchinson, 1964–1967; Grondona, 1984; Zardini, 1973). El género *Acaena* comprende subarbustos y herbáceas, generalmente leñosas en la base, decumbentes o extendidas, con las ramas floríferas a menudo erectas. Sus hojas son alternas, compuestas, imparipinnadas, dentadas o aserradas, con estípulas envainadoras en la base. Las flores son pequeñas y están dispuestas en capítulos o en espigas, en el ápice del tallo; pueden ser verdes, rojas o blancas y estar acompañadas de brácteas; el tubo del cáliz es persistente y puede ser desnudo, tuberculado o armado con espinas y garfios; los pétalos están ausentes y los estambres son 1–10, sésiles, insertos en la garganta del cáliz; el ovario es perígino, dialicarpelar, el estilo es subterminal, corto, con estigma peltado, espatulado o dilatado y fimbriado o penicilado. El óvulo es solitario y péndulo, el fruto es un aquenio que va incluido en el tubo del cáliz endurecido o esponjoso, tuberculado o con cerdas, conjunto que recibe el nombre de cupela (Grondona, 1964, 1984; Hutchinson, 1964–1967). Según Spujt (1994), el tipo de fruto de *Acaena* corresponde a un diclesium. Este difiere de otros antocarpos secos por el pericarpio que está incluido dentro del exocarpo, el que usualmente deriva del perianto. En frutos derivados de un ovario ínfero, como es el caso de *Acaena*, la presencia de costillas o alas sobre el exocarpo es usualmente considerada derivada desde un perianto acrescente. Sin embargo, es un nombre poco utilizado, y para esta revisión se conserva el nombre de cupela, por ser de uso más frecuente en los textos.

En cuanto a las características de las flores, éstas son poco vistosas, con perianto reducido, generalmente de color verde, o café oscuro a rojo, o bien puede estar ausente o ser deciduo (Faegri & van der Pijl, 1971). La efectividad de los estigmas como captadores de polen se encuentra incrementada por la exposición hacia afuera, más allá de las brácteas o el perianto. También es importante la exposición de las anteras, para que el aire pueda llevar lejos el polen. Los estambres se caracterizan por presentar filamentos largos, dejando a las anteras fuera del perianto. Como una condición no morfológica para el éxito de la anemofília, está lo que se refiere al número de individuos componentes de una población, los cuales dependen de cierta masividad de polen incidente (Faegri & van der Pijl, 1971). Todas las características mencionadas para plantas con polinización anemófila, se presentan en el género *Acaena*, y debido a la simplicidad de estas, es que los caracteres de mayor utilidad son los reproductivos, en especial los caracteres de la cupela, debido a una mayor diversidad y riqueza de formas y ornamentaciones. Además, son de utilidad la disposición de las flores y las cupelas y la forma de la inflorescencia y de la infrutescencia.

Un carácter presente en algunas especies de *Acaena* es la formación de flores cleistógamas. Estas se caracterizan por una reducción en el tamaño y número de las piezas florales, en especial las anteras, y por modificaciones en el perianto (Frankel & Galun, 1977; Lord, 1981). En las especies chilenas del género, se observa un gradiente de tipos florales, desde chasmógama a cleistógama, dentro de un mismo individuo; las flores consideradas cleistógamas no presentan una modificación notoria que las haga

claramente distintas de las chasmógamas, lo más evidente son la ubicación y protección por las vainas foliares. Esta transición de tipos florales indica que la cleistogamia es una condición derivada de la chasmogamia (Frankel & Galun, 1977).

Se considera que son factores ambientales, tales como temperatura, sequedad, humedad, luminosidad, los responsables de la formación de flores cleistógamas (Uphof, 1938; Lord, 1981). Es probable que algunos de estos factores, solos o en conjunto, provoquen la formación de flores cleistógamas en algunas de las especies presentes en el país. Sin embargo, esto no explica la falta de ellas en algunas especies que habitan las mismas áreas que aquellas que sí poseen flores cleistógamas. Sin embargo, Lord (1981) afirma que en condiciones naturales, ambas formas, chasmógamas y cleistógamas, aparecen en un mismo momento durante el ciclo de vida de la mayoría de las plantas.

En cuanto al período de floración y fructificación se observó que no existe una etapa distinta de la otra, ambas ocurren casi simultáneamente, por lo cual sólo se señala el período de fructificación ya que además es el más útil para la identificación.

Dentro de los caracteres vegetativos, los más útiles fueron la forma y disposición de los folíolos. *Acaena alpina* Poepp. ex Walp. y *A. splendens* Hook. et Arn. son muy parecidas, pero si no presentan frutos se pueden diferenciar debido a que los folíolos de la primera se disponen de forma digitada y en *A. splendens* se presentan de manera pinnada. Para otras especies en cambio es necesario observar tanto caracteres del fruto como de las hojas.

Otros caracteres vegetativos cuantitativos como longitud del pedúnculo floral, tamaño de las hojas y de los folíolos, tamaño de las brácteas basales entre los más notorios, son altamente variables en la mayoría de las especies, por tanto su utilidad es mínima. Esto ha provocado que tanto Bitter (1910) como Philippi (1862, 1863, 1872, 1893) describieran un gran número de especies y variedades, generando un gran número de nombres que han sido sinonimizados (Grondona, 1964; Walton, 1975).

Ha sido un largo trabajo la revisión de las descripciones de los taxa creados por Bitter, y reconocer que correspondían a un número mucho menor de especies. Como ya se comentó, este autor describió cerca de 100 taxa para Chile, lo que refleja el estrecho concepto de especie que tenía. No fue posible acceder a todos los materiales tipos de los taxa descritos por Bitter, debido a que la mayoría de ellos se encontraban en el herbario de Berlín, el cual fue destruído en la Segunda Guerra Mundial. Sin embargo, las evidentes similitudes morfológicas de dichos taxa, reconocidas mediante las completas y exactas descripciones realizadas por Bitter, además de la localización de los lugares de colecta en áreas donde sólo crece determinada especie, permiten considerar que es altamente probable que dichos taxa principalmente infraespecíficos, se refieren a la especie bajo la cual se encuentran.

Simpson (1979), refiriéndose a la revisión del género *Polylepis* realizada por Bitter (1911), señala que el concepto tipológico del autor y su tratamiento de individuos más que de poblaciones, dejó una fragmentación taxonómica que hace imposible identificar nuevas colectas. Obviamente esta situación es la misma para el género *Acaena*.

La especie más citada por la literatura es *Acaena magellanica* (Lam.) Vahl, ya que presenta un gran variabilidad morfológica, además de anormalidades como desarrollo de capítulos subsidiarios, flores pediceladas, capítulos incompletos, poca elongación del escapo y de los entrenudos lo que produce hojas en roseta (Walton, 1979).

Uno de los mayores problemas fue determinar a qué especie correspondían algunos individuos, debido a la combinación de caracteres que presentaban. Se observaron individuos que compartían caracteres de *Acaena magellanica* y *A. ovalifolia* Ruiz et Pav., de los cuales la mayoría proviene de la XII Región, donde ambas especies son muy abundantes. A pesar de ésto, Grondona (1964) y Walton y Greene (1971) consideran que estas especies, aunque habitan juntas, aparentemente no hibridizan, como lo reafirma Walton (1979). En general, la variación morfológica de una especie está ligada a la plasticidad fenotípica o a la diversidad genética (Briggs & Walters, 1984), luego se considera necesario realizar un estudio más profundo entre las especies *A. magellanica* y *A. ovalifolia* que habitan en Chile, analizando previamente el complejo *A. magellanica*, utilizando información de datos moleculares para verificar la existencia o no de divisiones infraespecíficas reconocibles, o si sólo corresponde a una gran variación morfológica debida a plasticidad fenotípica y con esto también establecer las causas de la variabilidad presente en algunas especies.

Micromorfología

Marticorena (2000) reconoció patrones celulares en la epidermis de la cupela, y determinó tres tipos básicos, los que se corresponden con las secciones y subgéneros a las que pertenecen las especies, niveles taxonómicos que han sido circunscritos sobre la base de caracteres morfológicos tradicionales, y que fueron denominados como acaena, ancistrum y axillares.

Distribución Geográfica

La familia Rosaceae presenta una distribución cosmopolita (Heywood, 1985), restringida esencialmente a climas templados. Se la considera originaria de Laurasia y que luego llegó a Sudamérica, a Malasia, desde allí a la región Pacífico-Australiana, y por último a Africa, esto unido a su predominancia en Europa, Norteamérica y Asia continental (Kalkman, 1988). Respecto del género *Acaena*, al parecer la hipótesis más aceptada es la que considera su evolución a partir de una Sanguisorbeae primitiva, que llegó al sur de Sudamérica relativamente temprano, mediante dispersión a larga distancia, y que luego desde allí se dispersó ampliamente a la región Antártica y al norte (Raven & Axelrod, 1974), hasta alcanzar América Central y California con 3 especies (Moore, 1972).

La dispersión de plantas insulares de *Acaena* es indudablemente debida a las aves marinas, mientras que la abundancia y amplia distribución de las especies continentales, en especial de Sudamérica, es debida a la adhesión en las plumas de aves, al pelo de los animales salvajes, tales como viscachas (Grondona, 1964), y también a ganado doméstico (Johow, 1896; Skottsberg, 1954) y a la vestimenta (Ridley, 1930). La teoría de que el género se desarrolló en el hemisferio sur, está fundamentada por el número de taxa que se presentan mayoritariamente en el sur de Sudamérica, con aproximadamente 22 especies (Grondona, 1964, 1984), Nueva Zelandia (16 especies, Macmillan, 1988), Australia (5 especies, Beadle et al., 1982). Luego, un menor número en América Central y México, y una especie en Hawaii (*Acaena exigua* A. Gray), California (*A. californica* Bitter), Sudáfrica (*A. latebrosa* Aiton), y en islas subantárticas, e.g. Kerguelen, South Georgia, Macquaire y Falkland (*A. magellanica*) (Greene, 1964; Moore, 1968; Walton, 1979, Pisano, 1984).

En Chile, el género se distribuye ampliamente, ocupando todo el territorio, con un mayor número de taxa presente desde la V a la XII Región. Se las puede encontrar en variados ambientes, que van desde lugares secos hasta húmedos, entre rocas, suelos arenosos o en vegas. En Chile insular, el Archipiélago de Juan Fernández posee tres especies, una endémica, *Acaena masafuerana* Bitter, y dos nativas de Chile continental, *A. argentea* Ruiz et Pav. y *A. ovalifolia*. Estas últimas se comportan como malezas muy agresivas, cubriendo terrenos de pastoreo, praderas en las costas, claros en el bosque, terrenos húmedos a orillas de los esteros (Johow, 1896; Matthei, 1995; Reiche, 1897; Skottsberg, 1954).

En general las especies siguen la distribución impuesta por la diagonal árida, presentando un mayor número de especies en la zona sur de Chile, comenzando desde el sur-este de Argentina, en especial la zona patagónica, cruzando los Andes en sentido noroeste.

Historia del Género

El género *Acaena* fue propuesto por Mutis en 1771 y válidamente publicado por Linnaeus (1771: 200) basado en la especie *A. elongata* L., material proveniente de México según Linnaeus, pero en realidad de Colombia (introducción de Stearn, Linnaeus, 1771). Ruiz y Pavón (1798–1802) describieron 6 nuevas especies de las cuales 4 se encuentran en Chile. El primero en subdividir el género fue de Candolle (1825), quien reconoció dos secciones que denominó *Euacaena* DC. y *Ancistrum* (J. R. Forst. et G. Forst.) DC., basándose en la posición de las espinas en la cupela. Este último nombre fue tomado del género *Ancistrum* publicado por J. R. Forster y G. Forster en 1775, el que Vahl (1804–1805) consideró sinónimo de *Acaena*. Gay (1847) incluyó 12 especies en la sección *Acaena* y 9 en *Ancistrum*, describiendo dos nuevas especies, una para cada sección. Sin embargo este trabajo entrega sólo descripciones, con un breve comentario sobre distribución, siendo algunas descripciones sólo copia de la original. También hace referencia a las similitudes entre las especies y comenta sobre las características que permiten reconocerlas de otras afines. Hooker (1844–1847), reconoció 10 especies sin considerar secciones y describió 3 especies nuevas, dos de las cuales son citadas para Chile. Weddell (1855–1861) utilizó las secciones de de Candolle y a su vez las subdividió basándose en el tipo de inflorescencia, ya sea espiciforme o capituliforme, donde 11 de las 16 especies son citadas para Chile. En este trabajo sólo se entregan breves descripciones, con algunas observaciones sobre las similitudes entre especies. Philippi entre los años 1857 y 1893 describió 22 especies para Chile, de las cuales varias fueron basadas sobre material incompleto, ya sea sin flores ni frutos o con flores inmaduras, caracteres que él mismo consideraba importantes para el reconocimiento de las especies, lo que de este modo hace que las especies descritas sean de un valor dudoso. Citerne (1897) hizo un estudio del género *Acaena* en el que incluyó descripciones de los órganos vegetativos y reproductivos, morfología y anatomía de los frutos y semillas. También se refirió a las afinidades con algunos géneros como *Polylepis*, *Sanguisorba* y *Poterium*, y presentó un esquema de clasificación donde dividió al género en 7 secciones, basándose en el tipo de inflorescencia, la posición axilar o terminal de las

ramas floríferas y la posición de las espinas en la cupela; estas secciones son: *Acaena* (como *Pleurostachya* Citerne), *Lachnodia* Citerne, *Brachycephala* Citerne, *Pleurocephala* Citerne, *Acrostachya* Citerne, *Acrocephala* Citerne, *Anoplocephala* Citerne. Reiche (1897) utilizó las secciones publicadas por de Candolle (1825), pero las elevó al rango de subgénero; de tal modo reconoció en el subgénero *Acaena* (como "Euacaena") 15 especies y en *Ancistrum* 10 especies, considerando como carácter principal el tipo de inflorescencia y como segundo carácter la posición de las espinas en la cupela, siendo el primero en confeccionar una clave para el reconocimiento de las 24 especies reconocidas para el país. Bitter (1910) realizó una monografía del género aceptando algunas secciones creadas por Citerne y dividió al género en dos grandes grupos, Axillares y Terminales, los cuales el subdividió considerando numerosos otros subgrupos dentro de *Acaena*. No obstante, la mayoría presenta límites poco claros, donde especies que pertenecían a distintas subgrupos (secciones según Bitter) son sinónimos de una sola especie, e.g. Subantarcticae, Dolichanteroideae o Glaucophyllae, que en términos generales sólo comprende variantes de *A. magellanica*. En el presente trabajo sólo se consideró la división del género hasta sección. Del tratamiento que hace Bitter para el género, se reconoce que alrededor de 100 serían los taxa presentes en Chile, distribuídos en aproximadamente 60 especies con subespecies y variedades, muchas de las cuales fueron sinonimizadas por Grondona (1964) y Walton (1975). Estos autores consideraron que Bitter utilizó caracteres extremadamente variables e inadecuados para la diferenciación taxonómica de los taxa infraespecíficos, tales como la pilosidad de los tallos, número y tamaño de los folíolos, longitud del pedúnculo, o que sólo utilizó poblaciones femeninas, las que correspondían a especies ya descritas, como es el caso de *A. magellanica*.

Grondona (1964) hizo una revisión del género para Argentina, donde 14 de las 20 especies, son compartidas también con Chile. Fue el primero en incluir cortes anatómicos de frutos, que desde el punto de vista taxonómico no fueron una herramienta útil para la identificación de especies, debido a que el número de aquenios dentro de las cupelas puede variar de uno a cuatro en una misma planta, esto unido a que las secciones transversales de las cupelas pueden presentar distintas formas, también dentro de una misma planta. Este trabajo se caracteriza por reducir drásticamente el número de especies reconocidas por Bitter y algunas de Philippi y Gay. En 1984, Grondona, reconoce a las especies *Acaena antarctica* Hook. f. y *A. tenera* Alboff que en 1964 había considerado sinónimos o no había podido identificarlas con precisión. Walton (1975) completó la ya larga lista de sinónimos para las especies *A. magellanica* con 28 especies sinonimizadas, *A. antarctica* 9 especies, y *A. ovalifolia*, *A. lucida* (Aiton) Vahl y *A. pumila* Vahl, con una especie cada una. El autor se basó en material tipo y en la descripción original, y concordó con el amplio concepto de especie adoptado por Grondona (1964). El catálogo de la flora vascular de Chile (Marticorena & Quezada, 1985) está basado en la opinión que se han formado los autores a través de la literatura y su experiencia. En él señalan que existen géneros que no han sido revisados desde hace mucho tiempo, algunos de los cuales presentan una nomenclatura caótica y que luego de una revisión pueden cambiar, dentro de los cuales se puede mencionar a *Acaena*. Luego en un trabajo estadístico sobre la flora vascular de Chile (Marticorena, 1991), se entregan valores expresados en número de taxa, de géneros, de especies, y para *Acaena* se listan 22 taxa que corresponden alrededor del 40% de la familia en el país y que lo constituye en el género con mayor número de representantes dentro de ella. Los trabajos antes indicados han generado gran cantidad de información sobre el género; sin embargo fueron realizados, ya sea para áreas que presentan algunas especies que también crecen en Chile (Grondona, 1964, 1984) o son muy extensos, con gran cantidad de taxa que han sido basados en caracteres poco confiables por su variabilidad.

Taxonomía

Acaena Mutis ex L., Mant. pl. 2: 145, 200. 1771. TIPO: *Acaena elongata* L.

Ancistrum J. R. Forst. et G. Forst., Char. Gen. 3, tab. 2. 1775. TIPO: *Ancistrum anserinifolium* J. R. Forst. et G. Forst. [= *Acaena anserinifolia* (J. R. Forst. et G. Forst.) J. Armstr.]

Hierbas perennes, generalmente leñosas en la base. Hojas alternas, imparipinnadas, con vainas foliares en la base, a veces acompañadas por apéndices estipulares de forma variable; folíolos enteros, incisos, aserrados o pinnatífidos, sésiles. Ramas floríferas terminales o axilares; inflorescencia capituliforme o espiciforme. Flores hermafroditas o algunas pistiladas, chasmógamas o cleistógamas; hipantio profundamente cóncavo, angosto en el ápice, con un fino reborde donde se disponen las piezas florales; sépalos (4) 5 (6), persistentes, lanceolados u ovados a oblongos u orbiculares; pétalos ausentes; estambres 2–6, anteras púrpuras o amarillentas; estilo con estigma oblongo o lanceolado u orbicular, laciniado. Cupela ovoide u oblongoide a obcónica o globosa, glabra a serícea, lisa o costillada, con o sin espinas de largo variable, que pueden o no terminar en gloquidios; aquenio 1–2.

Clave para las Secciones del Género *Acaena* en Chile

1a. Inflorescencia capituliforme, globosa, multiflora; cupelas con 2–4 espinas en el ápice.
  2a. Cupelas obcónicas, pubescentes, no glandulares; espinas más largas que el ovario; epidermis de la cupela con límite celular levantado . . . . Secc. **Ancistrum**
  2b. Cupelas ovoides, con tricomas glandulares o glándulas sésiles en la superficie; espinas de longitud tamaño o más cortas que el ovario; epidermis de la cupela con límite celular hundido . . . . Secc. **Acrobyssinae**
1b. Inflorescencia espiciforme, subglobosa o alargada, o también de capítulos paucifloros; cupelas con 3 a numerosas espinas, con espinas rudimentarias o sin espinas.
  3a. Cupelas sin espinas o con espinas rudimentarias de aspecto giboso . . . . Secc. **Pleurocephala**
  3b. Cupelas con espinas notorias, no gibosas.
    4a. Cupela con numerosas espinas cortas, de igual largo, con gloquidios gruesos; cara inferior de la hoja con células papilosas . . . . Secc. **Subtuspapillosae**
    4b. Cupela con espinas de distinto largo, con y sin gloquidios; cara inferior de la hoja sin células papilosas.
      5a. Cupela con 3–4 espinas apicales, sin gloquidios; células epidérmicas de la cupela con el límite celular acanalado, pared anticlinal ondulada, pared periclinal convexa . . . . Secc. **Patagonicae**
      5b. Cupela con más de 4 espinas de largo variable irregularmente dispuestas en la superficie, con y sin gloquidios; células epidérmicas de la cupela con el límite celular levantado, grueso, pared anticlinal recta a curva, pared periclinal plana . . . . Secc. **Acaena**

1. Acaena secc. **Ancistrum** (J. R. Forst. et G. Forst.) DC., Prodr. 2: 592. 1825. TIPO: *Ancistrum anserinifolium* J. R. Forst. et G. Forst., Char. Gen. Pl. 3, tab. 2. 1775. [= *Acaena anserinifolia* (J. R. Forst. et G. Forst.) J. Armstr.]

Inflorescencia capituliforme, globosa, densa. Cupela obcónica, pubescente, con 2–4 espinas largas con gloquidios en el ápice. Hojas con estípulas.

Especies en Chile: *A. argentea, A. magellanica, A. ovalifolia.*

2. Acaena secc. **Acrobyssinae** Bitter, Biblioth. Bot. 17(74): 49. 1910. TIPO: *Acaena acrobyssina* Bitter.

Acaena secc. *Brachycephala* Citerne, Rev. Sci. Nat. Ouest 7(2): 39. 1897. TIPO: *Acaena microcephala* Schltdl. [= *Acaena antarctica* Hook. f.]

Inflorescencia capituliforme, pequeña. Cupela ovoide, con tricomas glandulares o glándulas sésiles esféricas en la superficie, con 4 espinas cortas con gloquidios, en el ápice. Hojas con estípulas.

Especies en Chile: *A. antarctica, A. masafuerana, A. tenera.*

3. Acaena secc. **Pleurocephala** Citerne, Rev. Sci. Nat. Ouest 7(2): 39. 1897. TIPO: *Acaena lucida* (Aiton) Vahl.

Inflorescencia en capítulo paucifloro. Cupela ovoide, con tricomas lanosos, sin espinas o algunas rudimentarias. Hojas sin estípulas.

Especies en Chile: *A. lucida.*

4. Acaena secc. **Subtuspapillosae** Bitter, Biblioth. Bot. 17(74): 38. 1910. TIPO: *Acaena pumila* Vahl.

Inflorescencia al principio espiciforme y reunida, alargada en estado fructífero. Cupela ovoide, glabra, totalmente cubierta de espinas cortas, de igual tamaño, con gloquidios. Hojas glabras, sin estípulas; cara inferior del folíolo con células papilosas.

Especies en Chile: *A. pumila.*

5. Acaena secc. **Patagonicae** A. E. Martic., Novon 9: 227. 1999. TIPO: *Acaena patagonica* A. E. Martic.

Inflorescencia espiciforme corta, alargada en estado fructífero, con glomérulos dispersos a lo largo del pedúnculo. Cupela ovoide, glabra a pilosa, con 3–4 espinas apicales, sin gloquidios. Hojas pilosas, sin estípulas.

Especies en Chile: *A. patagonica.*

6. Acaena secc. **Acaena**, Mant. Pl. 2: 145. 1771. TIPO: *Acaena elongata* L.

Inflorescencia generalmente espiciforme, elongada o subglobosa, raro de capítulos globosos. Cupela ovoide, obcónica o piriforme, generalmente pubescente y con numerosas espinas en toda la superficie, la mayoría de las veces dispuestas en costillas notorias, con o sin gloquidios. Hojas en general sin estípulas o con estípulas rudimentarias.

Especies en Chile: *A. alpina, A. caespitosa* Gillies ex Hook. et Arn., *A. integerrima* Gillies ex Hook. et Arn., *A. leptacantha* Phil., *A. macrocephala* Poepp., *A. pinnatifida* Ruiz et Pav., *A. platyacantha* Speg., *A. poeppigiana* Gay, *A. sericea* J. Jacq., *A. splendens, A. trifida.*

Clave para las Especies de *Acaena* en Chile

1a. Inflorescencia capituliforme, esférica, cupela obcónica, ovoide u obovoide, con 2–4 (raro más) espinas aciculares, de base angosta, apicales, con fuertes gloquidios.
2a. Inflorescencias e infrutescencia de más de 6.5 mm de diámetro, cupela obcónica, pubescente, sin tricomas glandulares; espinas más largas que el ovario.
3a. Cupela con tricomas tiesos, caedizos, de color amarillo pálido, con 2 (raro 3) espinas; cabezuelas rojizas; folíolos oblongo-elípticos a elípticos . . . . **11. A. ovalifolia**
3b. Cupela con tricomas blandos, persistentes, blancos, con 4 (raro 3 ó 5) espinas; cabezuelas moradas o amarillas; folíolos linear-lanceolados u obovados.
4a. Folíolos linear-lanceolados, cara superior glabra, verde oscuro, cara inferior serícea, plateada . . . . **3. A. argentea**
4b. Folíolos obovados, cuneados, caras superior e inferior glabras a pubescentes, verde claro . . . . **9. A. magellanica**
2b. Inflorescencias e infrutescencia menores o iguales a 6.5 mm de diámetro, cupela ovoide u obovoide, con tricomas glandulares o glándulas sésiles esféricas; espinas casi del largo del ovario.
5a. Cupela con glándulas sésiles esféricas en la superficie del ovario, con un mechón de tricomas glandulares en la base de los folíolos, sin tricomas glandulares entre las cupelas . . . . . . **19. A. tenera**
5b. Cupela sin glándulas sésiles esféricas en la superficie del ovario, sin un mechón de tricomas glandulares en la base de los folíolos, con tricomas glandulares entre y en la base de las cupelas.
6a. Pedúnculo glabro o con pocos tricomas esparcidos; generalmente espinas más cortas que la mitad del largo de la cupela; habita sólo en Más Afuera . . . . **10. A. masafuerana**
6b. Pedúnculo pubescente a glabro; generalmente espinas más largas que la mitad del largo de la cupela; habita al sur del continente Sudamericano . . . . **2. A. antarctica**
1b. Inflorescencia espiciforme, corta o larga, cupela ovoide, oblongoide o piriforme, con 3–4 espinas de base ancha, dispuestas en el tercio superior y otras de menor tamaño entre las mayores, o totalmente cubierta de espinas de tamaño similar, con o sin gloquidios, o sin espinas.
7a. Cupela sin espinas o con espinas rudimentarias . . . . **7. A. lucida**
7b. Cupela con espinas notorias.
8a. Hojas seríceas, pecíolo más largo que la lámina.
9a. Folíolos con 3 pares de dientes grandes por lado, base cuneada . . . . **17. A. sericea**
9b. Folíolos enteros o incisos, base no cuneada.
10a. Cupela de 7–15 mm de largo, con espinas rojizas, blandas; raquis casi nulo, hojas de aspecto palmado . . . . **1. A. alpina**
10b. Cupela de 2.5–12 mm de largo, con espinas café-claro, duras; raquis notorio, hojas sin aspecto palmado.
11a. Plantas de no más de 13 cm de altura, folíolos partidas, cupela glabrescente, con numerosas costillas notorias, totalmente recorridas por espinas cortas con fuertes gloquidios . . . . **4. A. caespitosa**
11b. Plantas de más de 13 cm de altura, folíolos enteros o con algunos dientes pequeños, cupela pubescente, sin costillas notorias.
12a. Folíolos de color verde claro, enteros o con hasta 22 dientes pequeños; cupela oblongoide-elipsoide . . . . **18. A. splendens**
12b. Folíolos de color gris plateado, enteros o tridentados en el ápice; cupela ovoide-globosa . . . . **5. A. integerrima**
8b. Hojas glabras o pubescentes, pecíolo de igual largo o menor que la lámina.
13a. Folíolos orbiculares, lobulados, glabros . . . . **16. A. pumila**
13b. Folíolos aserrados o partidos en el ápice.
14a. Folíolos pinnatisectos, con 5–7 pares de segmentos linear-lanceolados.
15a. Hojas con pecíolo notorio, sin apéndices estipulares; cupelas dispuestas en una espiga larga, abierta, con espinas tiesas, duras . . . . **13. A. pinnatifida**
15b. Hojas sésiles, con apéndices estipulares desarrollados o rudimentarios; cupelas dispuestas en una cabezuela o espiga corta, con espinas flexibles.
16a. Inflorescencia en espiga contraída, esférica, de 13–45 mm de diámetro, cupelas con espinas pubescentes, con tricomas largos, blandos, glabras al ápice, sin gloquidios; apéndices estipulares rudimentarios **8. A. macrocephala**
16b. Inflorescencia en espiga corta, no contraída, de 2–4 cm de largo, que se alarga al madurar; cupelas con espinas glabras y sin gloquidios o espinas con tricomas retrorsos y gloquidios; apéndices estipulares desarrollados . . . . **6. A. leptacantha**
14b. Folíolos bi- a tripartidos.
17a. Folíolos de hasta 3.5 mm de largo, segmentos de los folíolos oblongo-elípticos, ápice obtuso, margen no revoluto . . . . **15. A. poeppigiana**
17b. Folíolos la mayoría mayores de 3.5 mm de largo, segmentos de los folíolos lineares a lanceolados, ápice agudo, margen revoluto.
18a. Cupela con 1–2 espinas por costilla, como alas aplastadas lateralmente, triangulares, cortas; superficie rugosa entre las cada costilla . . . . **14. A. platyacantha**

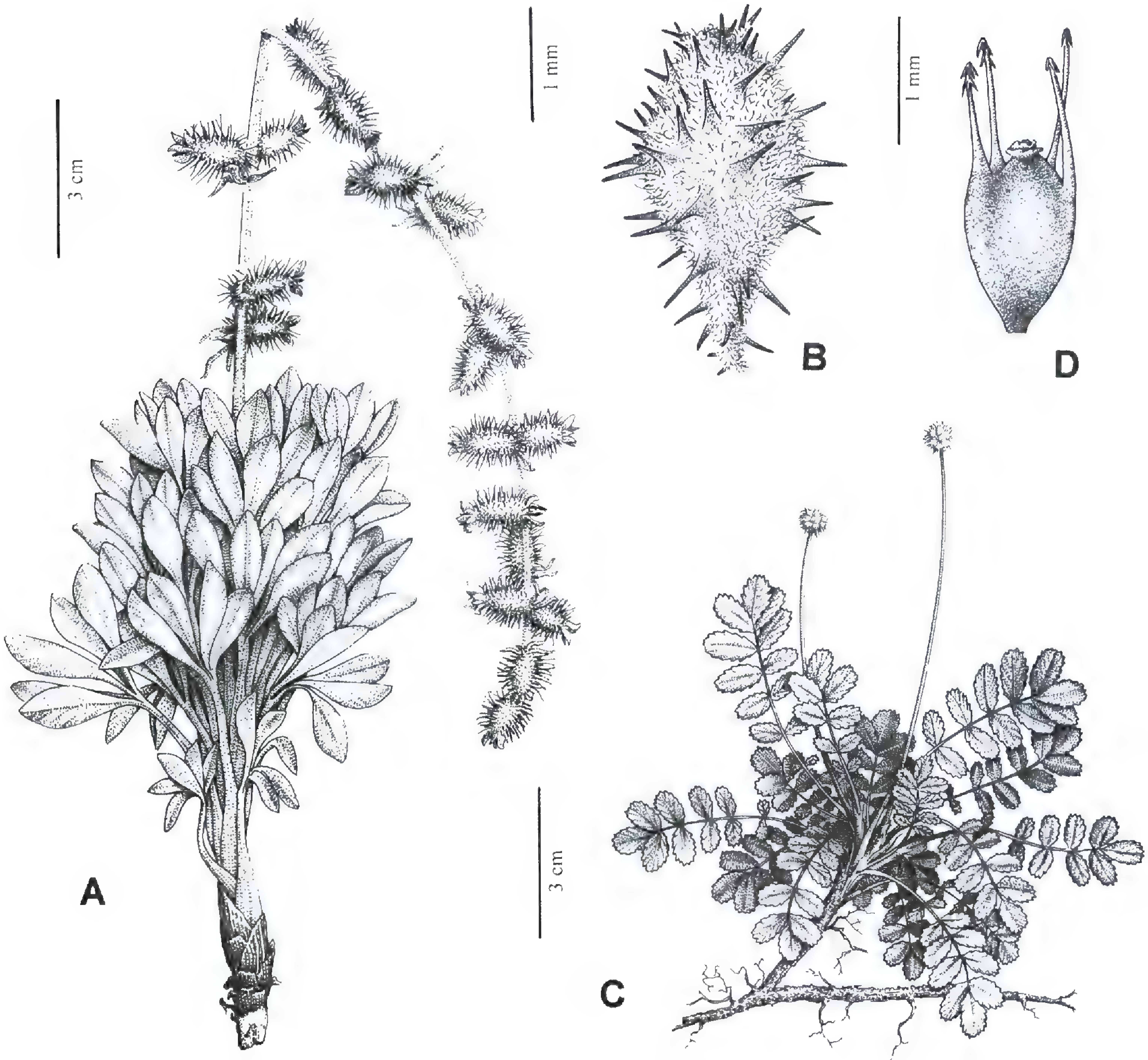

Figura 1. *Acaena alpina.* —A. Hábito. —B. Cupela (*A. Marticorena et al. 233*, CONC). *Acaena antarctica.* —C. Hábito. —D. Cupela (*Villagrán et al. 6855*, CONC).

18b. Cupela con espinas más o menos cónicas o subaciculares, sin superficie rugosa entre las espinas.
- 19a. Plantas gráciles; cupelas de 1.5–2.5 mm, dispuestas en una espiga corta, oblongoide, de hasta 6.5 mm de diámetro; costillas 3–4, con una espina subacicular por costilla, dispuesta en el tercio superior, raro una espina rudimentaria bajo ella . . . . **12. A. patagonica**
- 19b. Plantas robustas; cupelas de 2.5–6 mm, dispuestas en una espiga corta, redondeada, de más de 8 mm de diámetro; pedúnculo floral con hojitas dispersas a lo largo, costillas generalmente 5, con 2 espinas cónicas, de tamaño similar por costilla . . . . **20. A. trifida**

1. Acaena alpina Poepp. ex Walp., Nov. Actorum Acad. Caes. Leop.- Carol. Nat. Cur. 19, Suppl. 1: 326. 1843. TIPO: "Chile boreal inter fragmentas syenitica ad nives perpetuas. Estero del Peñón rajado. Cordillera de la Rosa. Debr. 1827," *Poeppig 517* (lectotipo, aquí designado, W!, las dos superiores). Figura 1A, B.

Acaena digitata Phil., Anales Univ. Chile 21: 445. 1862. TIPO: Chile. "Invernada de Maule," *Volckmann s.n.* (lectotipo, aquí designado, SGO-49861!).

Acaena digitata var. *latifoliolata* Bitter, Biblioth. Bot. 17(74): 89. 1910. TIPO: Chile. "Cordillera de Maule, 1855, *Ph. Germain s.n.*" (lectotipo, aquí designado, W-110760!; duplicado, G, foto 27423 en CONC!).

Acaena digitata var. *subpinnata* Bitter, Biblioth. Bot. 17(74): 90. 1910. TIPO: Chile. "Cordill. de Baucagna [sic],

1856–1857, *Ph. Germain s.n.*" (lectotipo, aquí designado, W-112652!).

Planta de 8–30 cm de alto; rizoma 4–5.5 mm de diámetro; tallos suberectos; entrenudos cortos, cubiertos por las vainas foliares. Hojas 2–7 cm de largo; 2 a 3 pares de folíolos, 1° y 2° par de folíolos separados por menos de 2 mm, raquis casi nulo, dándole un aspecto palmado o digitado, obovado-lanceolados, 21–26 mm de largo, el margen aserrado en el tercio superior, seríceos; vainas foliares con el dorso seríceo y la cara interna glabra; apéndices estipulares ausentes. Rama florífera terminal; pedúnculo de hasta 27 cm de largo, piloso; inflorescencia espiciforme, abierta, laxa, 4.5–10 cm de largo, con alrededor de 6–10 flores; brácteas basales lanceoladas a lineares, el margen irregular. Sépalos 5, ovado-oblongos, 4–5 mm de largo, la cara interna glabra, la cara externa pubescente con tricomas blancos, blandos, ascendentes; estambres 3–5, filamentos de ca. 3 mm de largo, anteras orbiculares, 1–1.5 mm de largo; estilo corto; estigma globoso, laciniado, ca. 1 mm de diámetro. Cupela ovoide-oblongoide, 7–15 mm de largo, sericea, totalmente cubierta por tricomas blancos, lanosos, que contrastan con las espinas blandas de color café rojizo, de tamaño similar, de 2–7 mm, con tricomas retrorsos esparcidos; aquenio 1.

Icones. Grondona, 1964: fig. 52; 1984: 438.

Fenología. Fructifica desde noviembre (*Grandjot s.n.*) a abril (*Zoellner 6476*).

Distribución y hábitat. Especie nativa que también crece en Argentina, habita en terrenos duros y secos, en los faldeos de cerros, desde la provincia de los Andes (Laguna del Inca) a la provincia de Malleco (Lonquimay), entre 350 y 3150 m de altitud (Fig. 11A).

Nombre común. Cepacaballo (*Hollermayer 712*), cadillo (*Jaffuel s.n.*).

Caracteres distintivos. Primer y segundo par de folíolos parten casi del mismo punto, dando el aspecto de hoja palmada. Cupela lanosa, oblongoide, con espinas café rojizas.

Acaena alpina pertenece a la Sección *Acaena.* Esta especie es muy semejante a *A. splendens*, especialmente en la pubescencia y forma de los folíolos, por lo que frecuentemente se confunden en estado vegetativo. No obstante, posee hojas de aspecto palmada y sus cupelas son de mayor tamaño, con espinas de color marrón-rojizas. Se le encuentra entre los 350 y 3150 m de altitud, aunque su mayor abundancia va desde los 2000 a 2800 m, en zonas cordilleranas de Chile central.

Bitter (1910) creó la subsección *Splendentes*, en la cual incluyó a *Acaena alpina*, *A. splendens* y *A. integerrima*, de acuerdo a que presentan pubescencia serícea, sus cupelas son ovoides a fusiformes, con dos a un aquenio, y los folíolos con el ápice inciso, con pocos dientes, o sin ellos.

Respecto de la tipificación, se eligió como lectotipo una carpeta depositada en W, la que presenta cinco plantas, de las cuales las dos superiores corresponden a *A. alpina*, y las demás a *A. splendens*. Posteriormente Bitter incluyó etiquetas aclaratorias y señala "diese beiden kleinen Pflanzen sind *A. digitata* Phil. die grossen: *A. splendens* H. et A. 1909 Bitter," donde se refiere a *A. alpina* como *A. digitata*, un sinónimo. Se eligió esta carpeta para lectotipificar, a pesar de la mezcla de material, debido a que corresponde con la información del protólogo, y que además la etiqueta está escrita a mano por Poeppig. Philippi (1862) describió *A. digitata*, y señala en el protólogo varios lugares, los cuales corresponden con dos carpetas, una colectada por Volckmann en Invernada Maule, y la otra por Germain, de la Cordillera de Linares. Se eligió como lectotipo la carpeta SGO-49861 puesto que presenta una espiga más desarrollada. Para la variedad *latifoliolata* Bitter, se estudió material de W y G, y se seleccionó como lectotipo la carpeta W-110760, que posee una planta bien desarrollada, con las cupelas casi completamente maduras. El protólogo de la variedad *subpinnata* Bitter, menciona un material de *Philippi 271* depositado en B, y presumiblemente destruido, y un material de Germain en W-112652, el cual fue elegido como lectotipo, que es una planta con las cupelas bien desarrolladas. El tipo de *Acaena digitata* Phil. var. *pleodactyla* Bitter, fue destruido en Berlín, y no existen isotipos. Sin embargo, he podido ver una foto del tipo en CONC (N 17998), que corresponde con *A. alpina*.

Material representativo examinado. CHILE. **V Región**: Los Andes, Laguna del Inca, *Arroyo 81277* (CONC). **Región Metropolitana**: Chacabuco, Tiltil, 20 Ene. 1920, *Jaffuel s.n.* (CONC); Santiago, Cerro Ramón, 15 Dic. 1931, *Grandjot s.n.* (CONC); Cerro Abanico, Nov. 1932 *Grandjot s.n.* (CONC); Cordillera, Cajón del Maipo, Baños Morales, *Weldt 697* (CONC); Maipo, Cordillera de Aculeo, 15 Ene. 1955, *Germain s.n.* (SGO). **VI Región**: Colchagua, Termas del Flaco, *Zoellner 6476* (CONC). **VII Región**: Curicó, Laguna de Teno, *C. Marticorena et al. 22* (CONC); Talca, Laguna del Maule, embalse de la laguna, *A. Marticorena et al. 233* (CONC). **VIII Región**: Ñuble, Camino a Termas de Chillán, 15 Ene. 1950, *Barros s.n.* (CONC). **IX Región**: Malleco, Lonquimay, *Hollermayer 712* (CONC).

2. Acaena antarctica Hook. f., Fl. Antarct. 1: 269. 1846. TIPO: Chile: "Hermite Island, cape Horn; on the mountains, rare, 1000 feet," *A. Menzies s.n.* (holotipo, K!). Figura 1C, D.

Acaena microcephala Schltdl., Linnaea 28: 463. 1857. TIPO: Chile. "Alia specimina fructifera lecta sunt Cordillera

de Ranco glareosis, Dic. 1854," *Lechler 2951* (lectotipo, aquí designado, G, foto 27425 en CONC!).

Acaena pearcei Phil., Anales Univ. Chile. 84: 626. 1893. *Acaena pumila* Phil., Linnaea 33: 67. 1864, non *Acaena pumila* Vahl, Enum. Pl. (Vahl). 1804. TIPO: Chile. "In andibus de Ranco dictis, et quidem in prato quodam c. 4500 p. s. m. elevato invenit ornat. R. Pearce," *R. Pearce s.n.* (holotipo, SGO-49890!).

Acaena tenuifolia Bitter, Biblioth. Bot. 17(74): 52. 1910. TIPO: Chile. "Andes de Villarrica. 1897," *F. W. Neger s.n.* (holotipo, M!).

Acaena pearcei var. *glabrinervis* Bitter, Biblioth. Bot. 17(74): 53. 1910. TIPO: Chile. "Andes, Villarrica. 1897," *F. W. Neger s.n.* (holotipo, M!).

Planta hasta 16 cm de alto; entrenudos cortos. Hojas 3.3–10.5 cm de largo; lámina en contorno obovado-lanceolada; 4–5 pares de folíolos, obovados, ápice truncado, base cuneada, asimétrica, 3.5–15.5 mm de largo, el margen pinnatipartido, con 7–13 segmentos, cubiertos por tricomas blancos en el raquis y el ápice de los segmentos; vainas foliares con tricomas largos, blancos en el dorso; apéndices estipulares cortos, como una pequeña elongación, de 1–3 mm de largo. Rama florífera terminal; pedúnculo hasta 13 cm de largo, glabro a pubescente; inflorescencia capituliforme, ca. 4.5 mm de diámetro, en fruto de hasta 7.5 mm; brácteas basales obovadas, ca. 2 mm de largo, anchas, con el ápice dividido irregularmente, con un mechón de tricomas tiesos en el ápice y el contorno. Sépalos 4, oblongo-lanceolados, ca. 1 mm de largo, con pequeñas manchitas rojas a lo largo, glabros; estambres 2–5, filamentos de ca. 0.5 mm de largo, anteras globosas, ca. 0.3 mm de largo; estilo corto, estigma globoso, aplastado, más ancho que largo, laciniado, ca. 0.5 mm de diámetro. Cupela ovoide, 1.5–2 mm de largo, con tricomas glandulares articulados, de color café rojizo, brillantes, desde la base, 4 espinas de base angosta, de 1–2 mm de largo, con fuertes gloquidios; aquenio 1.

Icones. Bitter, 1910: tab. 3 b, c. Grondona, 1964: fig. 1–3; 1984: fig. 445.

Fenología. Fructifica desde noviembre (*Pisano & Henríquez 6882*) a marzo (*Sparre & Constance 10705*).

Distribución y hábitat. Especie nativa, se la encuentra en bosques, en vegas o también en laderas de ceniza volcánica, y la zona austral en los sitios mejor drenados del turbal, entre cojines de *Bolax gummifera* (Lam.) Spreng. Se distribuye desde Osorno (Paso Puyehue) a la XII Región (Isla Wollaston, caleta Lientur), a altitudes entre 10 y 1800 m (Fig. 11A). También crece en Argentina (Grondona, 1964, 1984) y las Islas Falkland (Moore, 1968).

Caracteres distintivos. Capítulos de alrededor de 4.5 mm de diámetro; pelos glandulares café rojizos entre las cupelas, cupela glabra, con 4 espinas apicales pequeñas.

Acaena antarctica pertenece a la Sección *Acrobyssinae*. Es una especie cercana a *A. masafuerana*, de la cual es difícil de distinguir en estado vegetativo, ya que ambas son de pequeño tamaño, con tricomas glandulares de color dorado a rojizo entre las cupelas, folíolos con tricomas en las nervaduras, cupelas de tamaño similar con pequeñas diferencias en el largo de las espinas, color de las hojas y pubescencia del pedúnculo floral. Walton y Greene (1971), quienes se basaron en material tipo, consideraron que ambas especies poseen leves diferencias, como la pilosidad del escapo y de los folíolos, y el color de estos, pero que sin embargo son consistentes, y que en conjunto permiten separar una de otra, criterio aceptado en esta revisión. A esto se puede añadir, que las espinas de la cupela son más largas que la mitad de ella, a diferencia de *A. masafuerana* cuyas espinas no alcanzan la mitad de su largo.

Para *Acaena antarctica* se estudió el material tipo depositado en K, que presenta cinco plantas y tres etiquetas, dos de las cuales corresponde con la información del protólogo, es decir Menzies y Hermite Island. Dentro de los sinónimos, para *A. microcephala* existen dos carpetas referidas al protólogo con los números 3029 y 2951, de donde esta última colectada por Lechler y depositada en G, se eligió como lectotipo. Philippi (1864) describe *A. pumila* Phil., pero como ya existía *A. pumila* Vahl, le cambió el nombre a *A. pearcei* Phil. (Philippi, 1893), la que según el tipo depositado en SGO corresponde a *A. antarctica*. Grondona (1964) excluyó a *A. antarctica* de su revisión, y sólo menciona a *A. microcephala*, con los sinónimos *A. pumila* Phil., *A. pearcei* Phil. y *A. tenera* Alboff. Posteriormente, Walton y Greene (1971) demostraron que *A. microcephala* es sinónimo de *A. antarctica*. Para la variedad *A. antarctica* Hook. f. var. *argutidentata* Bitter, no fue posible localizar material tipo. No obstante, según la fotografía en Bitter (tab. 3 b, c, 1910), se considera que sólo corresponde a variaciones mínimas de la especie. Walton (1975) la incluye en un listado de sinónimos, y señala que reexaminó el material tipo de todas la especies excepto para *A. valida* Bitter. El tipo de última fue destruido en Berlín, pero he podido ver una foto en CONC (N° 3382) que claramente corresponde a *A. antarctica*. Para la especie *A. microcephala* Schltdl. var *minuta* Bitter, no fue posible localizar el tipo, sin embargo Walton (1975) la señala que vió el tipo, y la sinónimiza bajo *A. antarctica*.

Material representativo examinado. ARGENTINA. **Tierra del Fuego**: Río Olivia, *McSweeney 25* (HIP). CHILE. **IX Región**: Malleco, Tolhuaca, *Pennell s.n.* (SGO). **X Región**: Osorno, P. N. Puyehue, Antillanca, *Gardner & Knees 3889* (CONC); Volcán Osorno, *Sparre & Constance 10705* (CONC); Llanquihue, P. N. Vicente Pérez Rosales,

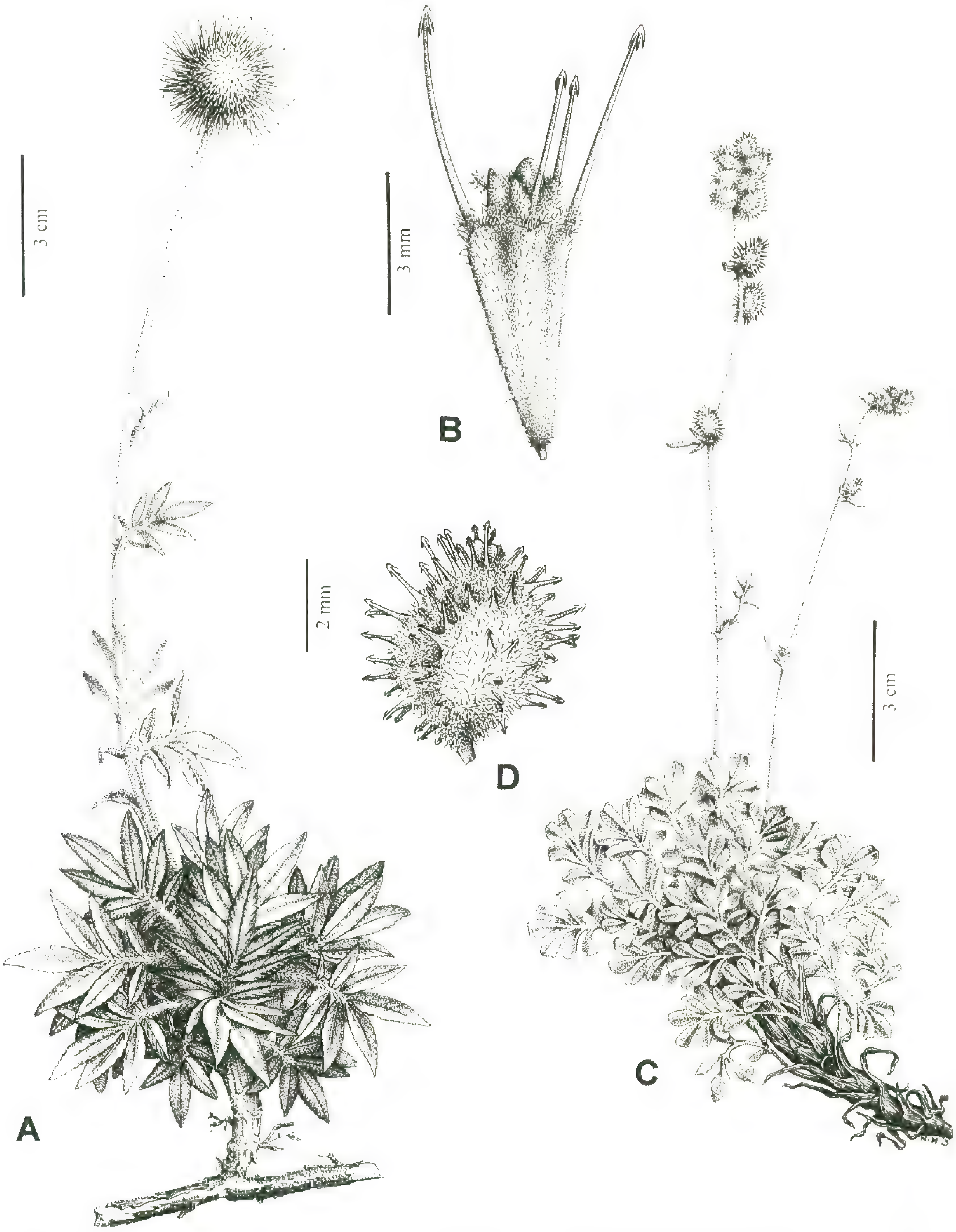

Figura 2. *Acaena argentea.* —A. Hábito. —B. Cupela (*Johow s.n.*, CONC 122372). *Acaena integerrima.* —C. Hábito. —D. Cupela (*C. Marticorena et al. 1254*, CONC).

Gardner 3450 (CONC); Chiloé, Lago Río Negro, *Villagrán et al. 6855* (CONC). **XI Región**: Aisén, Puyuhuapi, Cerro Tesoro, *Schwabe 70* (CONC). **XII Región**: Ultima Esperanza, Torres del Paine, Cerro Diente, *Arroyo & Squeo 870179* (CONC); Magallanes, Laguna El Parrillar, *Pisano 5739* (HIP); Tierra del Fuego, Cordón Baquedano, sector río Verde, *Pisano & Henríquez 6882* (HIP); Antártica Chilena, Isla Wollaston, Caleta Lientur, *Pisano 5120* (HIP).

3. Acaena argentea Ruiz et Pav., Fl. Peruv. Chil. 1: 67. 1798, non *Acaena argentea* Bertero ex

Steudel, Nomencl. Bot., ed. 2 (Steudel) i. 9. 1840. *Ancistrum argenteum* (Ruiz et Pav.) Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. (quatro ed.), 6: 230. 1824. TIPO: Chile. "Concepción, habitat abundè in locis uliginosis et arvis..., Itatae et Puchacay Provincianum, ad Ñipas, Yeguaraqui, Collico, Chequen, Loicaca, Pelchoquin et Chaymavida praedia," *Ruiz & Pavón s.n.* (holotipo, MA [Herbarium Peruvianum, Ruiz et Pavón, 10/77]!, foto 29606 en CONC!; isotipo, CONC-29701!). Figura 2A, B.

Acaena argentea var. *lanigera* Bitter, Biblioth. Bot. 17(74): 217. 1910. TIPO: Chile. "In graminosis siccis a Concepcion ad Antuco, 150–6000'," *Poeppig 684* (lectotipo, aquí designado W-359495!; duplicados, W!, WRSL!).
Acaena argentea var. *grandiceps* Bitter, Biblioth. Bot. 17(74): 217. 1910. TIPO: Chile. "Juan Fernandez (Challenger Exped., herb. Vindob.)," *Moseley s.n.* (holotipo, W-7351!).
Acaena argentea forma *viridis* Bitter, Biblioth. Bot. 17(74): 217. 1910. TIPO: Chile. "San Juan, in pascuis, Dec. 1852," *Philippi 311* (holotipo, BREM!) .
Acaena argentea forma *epargyrea* Bitter, Biblioth. Bot. 17(74): 217. 1910. TIPO: Chile. "Hacienda de San Juan (Valdivia), Nov. 1853," *Philippi 311* [colección mezclada, dos plantas en la parte inferior] (holotipo, BREM!).
Acaena argentea forma *nigricans* Bitter, Biblioth. Bot. 17(74): 217. 1910. TIPO: Chile. "Hacienda de San Juan, Dec. 1854," *Philippi 311* [colección mezclada, una planta en la parte superior] (holotipo, BREM!).
Acaena argentea var. *interrupte-pinnata* Bitter, Biblioth. Bot. 17(74): 217. 1910. TIPO: Chile. "Circa urbem Concepcion, herb. Delessert. et Vindob.," *Ph. Germain s.n.* (lectotipo, aquí designado, W-110756!; duplicado, G, no visto).
Acaena argentea var. *coriacea* Bitter, Biblioth. Bot. 17(74): 218. 1910. TIPO: Chile. "In monte ignivomo pr. Villarrica, herb. Monac., Rom., Vratisl.," *Lechler 318a* (lectotipo, aquí designado, W!; duplicado, WRSL!).
Acaena argentea var. *subcalvescens* Bitter, Biblioth. Bot. 17(74): 218. 1910. TIPO: Chile. "Concepcion, herb. Monac.," *F. W. Neger s.n.* (lectotipo, aquí designado, M!).
Acaena argentea var. *breviscapa* Bitter, Biblioth. Bot. 17(74): 218. 1910. TIPO: Chile. "San Cristobal, Eisenbahnstation, 26 Oct. 1896, herb. Stockh.," *P. Dusén s.n.* (lectotipo, aquí designado, S-8037!).

Planta hasta 35 cm de alto, rizoma de 3.5 mm de diámetro, tallo 2.5–4 mm de diámetro, cubierto por tricomas blancos, lanosos. Hojas en contorno obovadas, 4–12 cm de largo; 3–5 pares de folíolos, linear-lanceolados, 33–35 mm de largo, el margen aserrado a pinnatipartido, con ca. 10 segmentos, con un pequeño mucrón en el ápice, cara superior glabra, verde oscuro, inferior serícea, plateada; vainas foliares con igual pubescencia que las hojas, apéndices estipulares lineares, 10–18 mm de largo. Rama florífera terminal; pedúnculo de hasta 20 cm de largo, velloso; inflorescencia capituliforme, morada o amarilla, de hasta 14 mm de diámetro; brácteas basales lineares, 4–8 mm de largo. Flor chasmógama; sépalos 3–4, lanceolados, espatulados, con un mechón de tricomas en el ápice, de 1.5–2 mm de largo, cara interna brillante, cara externa cubierta por tricomas largos, transparentes, con un mechón en el ápice; estambres 2–5, filamentos hasta 2.5 mm de largo, anteras globosas, de 0.3–0.5 mm de largo; estilo corto, ca. 0.6 mm de largo, estigma oblongoide, laciniado, morado, de 1.4–2 mm de largo. Cupela obcónica, tetrágona, de color café rojizo, 11.5–14 mm de largo, pilosa, con tricomas blandos persistentes, blancos, con 4 espinas de base angosta en el ápice, desiguales, de 1.5–8.5 mm, glabras, con fuertes gloquidios; aquenio 1.

Icones. Grondona, 1964: fig. 8–10; 1984: fig. 442. Ruiz y Pavón, 1798: tab. 103, fig. b.

Fenología. Fructifica de octubre (*Lépez y Márquez 108*) a marzo (*Stuessy et al. 7255*).

Distribución y hábitat. Especie nativa, en Chile habita en suelos secos a húmedos, generalmente a la sombra, también a orillas de río. Crece desde Colchagua (La Rufina) a Palena, desde 5 a 1000 m de altitud, encontrándose como maleza en Juan Fernández, tanto en Más a Tierra como en Más Afuera (Fig. 11B). También se le encuentra en Argentina, Ecuador y Perú. Johow (1896) denominó a *Acaena argentea* como "la maleza más común en la isla," y Skottsberg (1921) la señaló como "la maleza más ampliamente distribuida y nociva" en Más a Tierra. Su reproducción vegetativa mediante largos estolones, esto unido a las espinas de sus frutos que le permiten adherirse a la piel de animales y a la ropa, la distinguen como la herbácea invasora más seria. Greimler et al. (2002a, 2002b) señalan que *A. argentea*, cubre el 9.21% de Más a Tierra, en una comunidad casi monodominante, siendo desde hace más de 100 años la invasora más común (Johow, 1896).

Nombres comunes. Cadillo (*Pfister 933*), trun (*Sparre 116*), amores secos, zarzaparrilla, proquín (Baeza, 1921).

Caracteres distintivos. Capítulos de alrededor de 1 cm de diámetro, cuando maduros de color café rojizo; folíolos lanceolados, cara inferior serícea, superior glabra; cupela con tricomas blancos, lanosos, con 4 espinas apicales.

Acaena argentea pertenece a la Sección *Ancistrum.* El material tipo corresponde a una colecta de Ruiz y Pavón depositada en el herbario de Madrid. La lámina en Ruiz y Pavón (1798: tab. 103, fig. b.) corresponde sin dudas a la especie. De los sinónimos

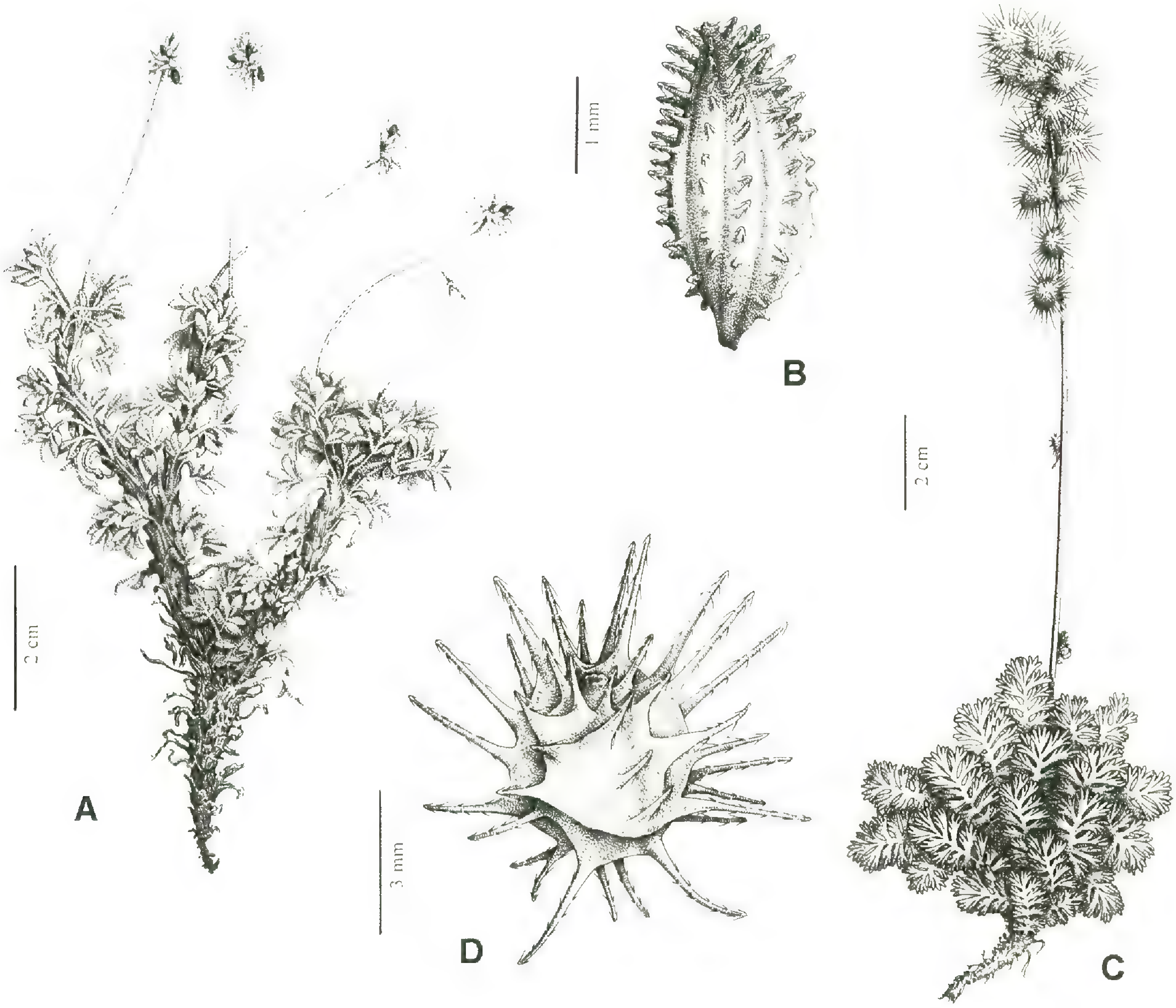

Figura 3. *Acaena caespitosa*. —A. Hábito. —B. Cupela (*Landrum 8437*, CONC). *Acaena leptacantha*. —C. Hábito. —D. Cupela (*Zöllner 5558*, CONC).

es interesante señalar el material tipo para las formas *epargyrea* y *nigricans* de la variedad *contracta*, *Philippi 311* depositado en BREM, el que pertenece a una carpeta con tres plantas, la superior corresponde a la forma *nigricans* y las dos inferiores a la forma *epargyrea*, con sus etiquetas con diferencias en las fechas, y que se relacionan a las dos formas, aunque la planta en la parte inferior derecha es difícil decir a cual la relacionó Bitter. Además existe otro material en BREM de *Philippi 311*, que corresponde a la forma *nigricans*, y que es idéntica a las demás. Para la variedad *lanigera* se eligió como lectotipo una carpeta de W que posee tres ejemplares, y además cuenta con etiquetas originales. Bitter (1910) describió dos variedades de *A. argentea*; var. *subcalvescens* y var. *breviscapa*, y en el protólogo de cada una menciona dos materiales distintos, depositados en diferentes herbarios. Para la variedad *subcalvescens* señala los herbarios M y G, de los cuales se pudo revisar el de M, que corresponde con la especie y que fue elegido como lectotipo. Para la variedad *breviscapa* señala los herbarios S y M, de los cuales se pudo examinar el espécimen de S-8037, que fue elegido como lectotipo.

Para algunos taxa no se pudo localizar material tipo, como por ejemplo el de *Acaena argentea* Ruiz et Pav. var. *gracillima* Bitter, que estaba depositado en B, y el que probablemente fue destruido. Otros taxa descritos por Bitter, *A. argentea* Ruiz et Pav. var. *brevifoliolata* Bitter y var. *pluribracteata* Bitter, sólo corresponden a leves variaciones de *A. argentea*, sin embargo no se pudo revisar material tipo. Para la última pude examinar la foto que aparece en la revisión de Bitter, la que sin duda corresponde a *A. argentea*.

Material representativo examinado. CHILE. **V Región**: Valparaíso, Juan Fernández, Más a Tierra, La Vaquería, *Crawford et al. 11863* (CONC); Más a Tierra, V. Colonial, *Sparre 116* (CONC); Más Afuera, Quebrada Casas, *Stuessy & Lammers 8443* (CONC). **VI Región**: Colchagua, La Rufina,

Fundo Bellavista, 4 Ene. 1951, *Ricardi s.n.* (CONC). **VII Región**: Curicó, Upeo, *Gunckel 70058* (CONC); Talca, Constitución, 15 Oct. 1890, *Reiche s.n.* (SGO); Linares, Parral, Digua, 7 Feb. 1971, *Silva s.n.* (CONC). **VIII Región**: Ñuble, Camino de Los Puquios a La Puntilla, *A. Marticorena et al. 272* (CONC); Ñuble, Atacalco, *Pfister 933* (CONC); Concepción, Ramuntcho, *Ricardi 367* (CONC); Concepción, Coronel, *Lépez y Márquez 108* (CONC); Arauco, Laraquete, *Gunckel 24096* (CONC); Biobío, Camino de Ralco a Lepoy, *A. Marticorena et al 298* (CONC), *Taylor et al. 10380* (CONC). **IX Región**: Cautín, Padre Las Casas, *Gunckel 38441* (CONC). **X Región**: Valdivia, San Juan, Ene. 1882, *Philippi s.n.* (SGO); Osorno, Trumao, *Hollermayer 625* (CONC); Llanquihue, Cayutué, 15 Ene. 1973, *Martínez s.n.* (CONC); Palena, 43.4 km SE Pto. Ramírez a Palena, *Stuessy et al. 7255* (CONC).

4. **Acaena caespitosa** Gillies ex Hook. et Arn., Bot. Misc. 3: 307. 1833. TIPO: Argentina. "El Paramillo de las Cuevas, El Alto de la Laguna, Andes of Mendoza and Chili," *Gillies s.n.* (lectotipo, aquí designado, K, foto 1227 en SGO!; duplicado, GL, foto 3688 en SGO!). Figura 3A, B.

Planta hasta 13 cm de alto, entrenudos cortos. Hojas 1.5–2.5 cm de largo, lámina en contorno obovado-orbicular; 2 pares de folíolos separados por más de 2 mm, ovado-orbiculares, 4.5–7.5 mm de largo, generalmente doblados a lo largo del nervio medio, el margen entero, seríceos, de color verde claro; vainas foliares con tricomas largos, blancos, tiesos, en la parte central de la cara externa y en el margen. Rama florífera terminal; pedúnculo hasta 9 cm de largo, velloso; inflorescencia globosa, subglobosa o espiciforme, de 7–10 mm de diámetro; brácteas basales oblongas, lanceoladas o lineares, de 2.5–4.5 mm de largo, pilosas en la cara externa, glabras en la interna. Sépalos 5, oblongo-lanceolados, de color verde claro, de 1.5–2 mm de largo, pubescente como las brácteas; estambres 2–5, anteras globosas, ca. 0.4 mm de largo; estigma lanceoloide, laciniado, ca. 1.2 mm de largo. Cupela oblongoide-lanceoloide, de 4–5 mm de largo, glabrescente, con alrededor de 10 costillas finas, recorridas por 8–11 espinas ca. 0.4 mm de largo, duras, con fuertes gloquidios y tricomas retrorsos; aquenio 1.

Icones. Grondona, 1964: 25–28; 1984: 443.

Fenología. Fructifica de diciembre (*Landrum 8437*) a enero (*Pfister s.n.*).

Distribución y hábitat. Planta nativa de la zona austral de Chile y Argentina (Grondona, 1964, 1984). Crece en suelo arenoso y en el país sólo se la ha encontrado en Tierra del Fuego (XII Región) a una altitud de 10 m (Fig. 11C).

Caracteres distintivos. Cupela con costillas cubiertas de espinas cortas con gloquidios gruesos; hojas seríceas, folíolos enteros, doblados por el nervio medio.

Acaena caespitosa pertenece a la Sección *Acaena*. Esta especie es afín a *A. alpina*, *A. splendens* y *A. integerrima*, principalmente por poseer pubescencia serícea, con folíolos generalmente enteros. Bitter (1910) agrupó a estas tres últimas especies en la subsección *Splendentes*, a diferencia de *A. caespitosa* que incluyó en la subsección *Dispersiflorentes*. De acuerdo a las características que comparte con las demás especies, se encuentra más relacionada con las especies mencionadas, que con las demás de su subsección, por lo que sería más adecuado incluirla dentro de la subsección *Splendentes*. Sin embargo, en esta revisión las subsecciones no han sido consideradas, debido principalmente a lo poco claro de sus límites. La descripción original señala a la especie para la zona de Los Andes de Mendoza y Chile; sin embargo, nunca se la ha colectado en el país a esas latitudes. Es probable que esto se deba a que los límites territoriales en esa época, no eran los de hoy, luego el material tipo se colectó en una zona que se consideraba chilena. Esta especie es bastante escasa, y sólo se le encuentra en la zona austral del país. Los materiales tipo están depositados en GL y K, con etiquetas que se corresponden con el protólogo. Ambos materiales están bien conservados y completos, pero se eligió el de K debido a que la carpeta incluye además un dibujo de la cupela, las espinas y las hojas.

Material representativo examinado. ARGENTINA. **Chubut**: Carrenleofu, Patagonia, *N. Illin. 1900* (LP). **Santa Cruz**: Lago Argentino, Dic. 1900, *S/C* (LP). **Tierra del Fuego**: Cabo Domingo, *Goodall 191* (LP). CHILE. **XII Región**: Magallanes, Punta Delgada, *Landrum 8437* (CONC); Tierra del Fuego, Bahía Felipe, 23 Ene. 1952, *Pfister s.n.* (CONC).

5. **Acaena integerrima** Gillies ex Hook. et Arn., Bot. Misc. 3: 306. 1833. TIPO: Argentina. "Near El Arroyo de los Potreros, Andes of Mendoza," *Gillies 113* (lectotipo, aquí designado, K!; duplicado, GL, foto en SGO-68707!). Figura 2C, D.

Acaena integerrima var. *subpilosicupula* Bitter, Biblioth. Bot. 17(74): 85, fig. 17. 1910. TIPO: Chile. "Patagonia australis-occidentalis: in litore maris, Eberhardt, herb. Stockh.," *O. Borge 157* (holotipo, S-03902!).

Planta hasta 35 cm de alto. Hojas en contorno obovadas, de 4.2–11 cm de largo; 2–4 pares de folíolos, obovado-lanceolados, de 4.5–13 mm de largo, tridentados en el ápice, seríceos, de color verde

claro a gris plateado; vainas foliares seríceas, sin apéndices estipulares. Rama florífera terminal, hasta 32 cm de largo; pedúnculos vellosos, de 20–31.5 cm de largo. Inflorescencia capituliforme, de 9.5–11 mm de diámetro, en fruto espiciforme o capituliforme, hasta 16 mm de diámetro; brácteas basales linear-lanceoladas, pubescentes a seríceas, 3–5 mm de largo. Sépalos 5–6, lanceolados, de 2.5–3 mm de largo, glabros en el interior, pubescentes en el exterior; estambres 3–5, anteras ovoides, ca. 0.7 mm de largo; estilo corto, raramente 2 estigmas, lanceoloides, laciniados, de 0.7–1 mm de largo. Cupela ovado-orbicular, de 2.5–7.5 mm, pilosa a vellosa, con costillas poco notorias, recorridas totalmente por duras espinas de tamaño similar, con gloquidios y tricomas retrorsos; aquenio 1.

Icones. Grondona, 1964: 53–57.

Fenología. Fructifica de noviembre (*Gunckel 50679*) a marzo (*Sparre & Constance 10873*).

Distribución y hábitat. Especie nativa, crece en cojines sobre faldeos secos, desde el Cajón del Maipo hasta Tierra del Fuego (Bahía Felipe), de 10 a 2000 m de altitud (Fig. 11B). También en Argentina.

Caracteres distintivos. Folíolos seríceos, de color gris plateado, enteros o tridentados en el ápice; cupela ovoide cubierta de espinas cortas con gloquidios.

Acaena integerrima pertenece a la Sección *Acaena*. Es una especie similar a *A. splendens*, debido a la pubescencia serícea y a lo parecido de sus cupelas. Grondona (1964) consideró a ambas especies distinguibles, sin embargo en 1984 sinonimizó a *A. integerrima* bajo *A. splendens*. De acuerdo a los especímenes examinados, ambas especies son distinguibles, debido a la forma, color y tamaño de los folíolos, y por la forma de la cupela. Los materiales originales de *A. integerrima* (*Gillies 113*) se encuentran depositados en K y GL, de los cuales se eligió como lectotipo el espécimen de K, debido a que es una carpeta con cuatro plantas completas, con etiquetas originales manuscritas que corresponden con los datos del protólogo. De los sinónimos, para la variedad *oligacantha* Bitter, el autor cita dos materiales, uno de *Philippi 274*, de la Cordillera de Linares, depositado en B y probablemente destruido, y el otro de *Germain*, de la Cordillera de Maule en el herbario FI. Ninguno de los dos se pudo localizar, sin embargo es posible que sólo presenten leves diferencias en relación al número de espinas de la cupela (*oligacantha*) que correspondería sólo a variaciones dentro de la especie.

Material representativo examinado. ARGENTINA. **Mendoza**: Cerro Guanacos, *Carrette 215* (LP). **Neuquén**: Cerro Chapelco, *Schajovskoy 94* (LP). **Río Negro**: Cerro Anecón, *Ferruglio 49* (LP). **Santa Cruz**: Güer Aike, Est. Las Viscachas, Co Sin Nombre, *T.B.P.A. 2638* (HIP). **Tierra del Fuego**: San Sebastián, 20 Abr. 1896, *Alboff s.n.* (LP). CHILE. **Región Metropolitana**: Cordillera, Cajón del Maipo, Las Vertientes, *Gunckel 50679* (CONC). **VII Región**: Talca, Entre Paso Pehuenches y Laguna del Maule, *Ricardi et al. 971* (CONC); Linares, Valle Botacura, *Schlegel 3577* (CONC). **VIII Región**: Biobío, Laguna de la Laja, *Ricardi & C. Marticorena 5735* (CONC). **IX Región**: Malleco, Camino Lonquimay–Paso Pino Hachado, km 13, *Ricardi & C. Marticorena 5658* (CONC); Lonquimay, 5 km SE del pueblo, *Sparre & Constance 10873* (CONC); Malleco, Cord. de las Raíces, cam. Lonquimay–Malalcahuello, *C. Marticorena et al. 1254* (CONC). **XI Región**: Coihaique, *Montero 5490* (CONC); General Carrera, Puerto Ibañez, 12 Feb. 1974, *Varas s.n.* (CONC). **XII Región**: Ultima Esperanza, Cerro Donoso, Río de las Chinas, *Arroyo et al. 870316* (CONC); Magallanes, Punta Dungeness, *Pisano 4531* (HIP); Tierra del Fuego, Punta Espora, *Pisano 3187* (HIP).

6. **Acaena leptacantha** Phil., Linnaea 33: 66. 1864. TIPO: Chile. "Cum *A. macrocephala* a cl. Gay in Andibus Talcaregue lecta confusa jacebat," *Philippi s.n.* (holotipo, SGO-49865!). Figura 3C, D.

Acaena capitata Phil., Anales Univ. Chile 84: 623. 1893. TIPO: Chile. "Habitat in Andibus ad Thermas Chillanenses, Febr. 1892," *Philippi s.n.* (holotipo, SGO-49905!).

Acaena macrocephala Poepp. var. *negeri* F. Duse, Nuovo Giorn. Bot. Ital. N.S. 12: 357. 1905. *Acaena leptacantha* var. *negeri* (F. Duse) Bitter, Biblioth. Bot. 17(74): 148, tab. 15a. 1910. TIPO: Chile. "Andes, Villarrica, 1897, Herb Monac.," *F. W. Neger s.n.* (holotipo, M!).

Acaena leptacantha var. *conferta* Bitter, Biblioth. Bot. 17(74): 147. 1910. TIPO: Chile. "From limits of vegetation, 1876, herb. Dessauer in herb. Monac.," *Neger 4639* (holotipo, M!).

Acaena leptacantha var. *longissima* Bitter, Biblioth. Bot. 17(74): 148, fig. 26. 1910. TIPO: Chile. "Patagonia media occidentalis: Vallis fluminis Aysén pars superior, 1000 m, 23 Feb. 1897," *Dusén 592* (holotipo, S-03-901!).

Acaena leptacantha subsp. *connectens* Bitter, Biblioth. Bot. 17(74): 149. 1910. TIPO: Chile. "In editissimis cordilleranum: Cauquenes et Talcaregue, prope nives perpetuas," *Gay 78* (holotipo, P, excepto la planta de la derecha, foto 34720 en CONC!).

Planta hasta 20 cm de alto; tallo cubierto por las hojas; entrenudos cortos. Hojas sésiles, de 11–37 mm de largo, lámina en contorno oblonga; 7–8 pares de folíolos, cuneados en la base, de 4.5–8 mm de largo, el margen pinnatisecto, 3 pares de segmentos, cara superior pilosa, envés pubescente a seríceo; vainas foliares pubescentes con tricomas largos, blancos; apéndices estipulares oblongo-lanceolados, pubescentes, de 1.8–2 mm de largo. Rama florífera terminal; pedúnculo hasta 17 cm de largo, piloso a seríceo; inflorescencia espiciforme corta, de 2–4 cm

de largo, abriéndose al madurar; brácteas basales ovado-oblongas a lineares, el margen irregular, de 3.5–5 mm de largo. Sépalos 5, ovado-oblongos, de 2.5–3 mm de largo, cara externa pilosa, interna glabra, con un mechón de tricomas en el ápice; estambres 2–3, anteras oblongoides a globosas; estigma globoso, laciniado, ca. 1 mm de diámetro. Cupela ovoide, de 1.5–1.7 cm de largo, pilosa, con la epidermis levantada, cubierta por espinas largas, de tamaño similar, de color café rojizo, con gloquidios y tricomas retrorsos o sin gloquidios y glabras; aquenio 1.

Icones. Grondona, 1964: fig. 33–36; 1984: fig. 147.

Fenología. Fructifica de enero (*Stuessy & Baeza 15560*) a abril (*Rodríguez y Parra 185*).

Distribución y hábitat. Planta nativa, crece en terreno húmedo, rocoso, formando matas cespitosas laxas. Se distribuye desde el volcán San José (Región Metropolitana) hasta Antillanca (X Región), en altitudes de 750 a 2500 m (Fig. 11C). También en Argentina.

Nombre común. Pimpinela (*Pfister s.n.*).

Caracteres distintivos. Folíolos pinnatisectos; espinas de la cupela con gloquidios y pelos retrorsos tiesos o sin gloquidios y glabras; inflorescencia espiciforme.

Acaena leptacantha pertenece a la Sección *Acaena*. Es una especie muy similar a *A. macrocephala*, difícil de diferenciar en estado vegetativo, pero que en estado reproductivo se distingue por las espinas de las cupelas con gloquidios, con tricomas retrorsos o totalmente glabras, y por la inflorescencia espiciforme corta, que en estado fructífero se abre y se hace más laxa. Bitter (1910) incluyó a ambas especies como los únicos taxa dentro de la Subsección Astenoglochinae, por presentar cupelas algo infladas, con la base de la espinas más o menos ensanchadas, las hojas apretadas en la base, con pelos algo amarillentos en la cara inferior. No obstante, se decidió no incluir divisiones menores que la sección, ya que los límites son poco claros.

Philippi (1857) describió *Acaena andina* Phil., de un material recolectado por *Germain s.n.* (holotipo SGO-49888!), el que posee semejanzas con *A. leptacantha*, lo que le daría prioridad en el nombre. Sin embargo, la inflorescencia se encuentra poco desarrollada, lo que deja la posibilidad de que también corresponda con *A. macrocephala* en su primera etapa de desarrollo, por lo tanto se prefirió dejar este taxón como dudoso.

En relación a los sinónimos, las variedades descritas por Bitter, *Acaena leptacantha* Phil. var. *grosseaculeata* Bitter, *A. leptacantha* Phil. var. *brachyacantha* Bitter y *A. leptacantha* Phil. var. *dolichacantha* Bitter, los materiales originales se encontraban depositados en Berlín, por lo cual presumiblemente fueron destruidos. Para los dos últimos taxa, se pudo examinar la foto que aparece en la revisión de Bitter (tab. 15 d y e, 1910), las que sin duda corresponde a *A. leptacantha*, es decir que el autor estableció sus variedades sobre la base de caracteres poco estables.

Material representativo examinado. ARGENTINA. **Neuquén**: San Martín de los Andes, cerro Chapelco, *Cabrera & Crisci 19193* (LP). **Río Negro**: P. N. Nahuel Huapi, cerro Tronador, *Fabris & Solbrig 784* (LP); Cerro Negro, *Fabris 2168* (LP). CHILE. **Región Metropolitana**: Cordillera, Volcán San José, *Gutiérrez 97* (SGO). **VII Región**: Curicó, Paso Vergara, *C. Marticorena & Matthei 1019* (CONC); Talca, Laguna del Maule, faldeo de los cerros, *Rodríguez & Parra 185* (CONC). **VIII Región**: Ñuble, Termas de Chillán, *Stuessy & Baeza 15560* (CONC); Biobío, Laguna del Laja, *Zoellner 5558* (CONC). **IX Región**: Malleco, Paso Pino Hachado, *C. Marticorena et al. 1417* (CONC); Cautín, Volcán Llaima, *Montero 4909* (CONC); Volcán Villarrica, Ene. 1954, *Pfister s.n.* (CONC). **X Región**: Valdivia, Volcán Mocho, *Montero 4985* (CONC); Osorno, Volcán Antillanca, *Ricardi & Matthei 5232* (CONC).

7. **Acaena lucida** (Aiton) Vahl, Enum. Pl. 1: 296. 1804, non *Acaena lucida* (Lam.) Vahl, Enum. Pl. 1: 296. 1804, nom. illeg. *Ancistrum lucidum* Aiton, Hort. Kew. I. 15. 1789. TIPO: Falkland Island, Antarct. Expedition 1839–1843, *J. D. Hooker 1827* (neotipo, aquí designado, G!). Figura 4A, B.

Ancistrum lucidum Lam., Tabl. Encycl. 1, Illustr. 1: 77, tab. 22, fig. 3. 1791. Nom. illeg., non *Ancistrum lucidum* Aiton, Hortus Kew. 1: 15. 1789.

Acaena lucida (Lam.) Vahl, Enum. Pl. 1: 296. 1804. Nom. illeg.

Acaena parvifolia Phil., Anales. Univ. Chile 84: 622. 1893; *Acaena lucida* var. *parvifolia* (Phil.) Reiche, Anales Univ. Chile 98: 161. 1897. TIPO: Argentina. "In Fuegia orientali lecta," *Ortega s.n.* (holotipo, SGO-49837!).

Acaena lucida var. *villosula* Bitter, Biblioth. Bot. 17(74): 61, tab. 5c, 1910. TIPO: Islas Falkland. "Insula Falkland," *J. D. Hooker s.n.* (lectotipo, aquí designado, P-106291!; duplicados, S-R8052!, CONC-29690!, P-106290!).

Acaena lucida var. *abbreviata* Bitter, Biblioth. Bot. 17(74): 61. 1910. TIPO: Argentina. "Fuegia orientalis: Rio Grande, pl. in reg. Magell.," *P. Dusén 377* (holotipo, S-R8050!).

Planta de 3.2–6.5 cm de alto; rizoma leñoso, ca. 3.5 mm de diámetro; tallo subdecumbente o erecto, con entrenudos cortos. Hojas en contorno linear-lanceoladas, de 1.7–2.2 cm de largo; 6–7 pares de folíolos, linear-lanceolados, profundamente bisectados, con el segmento superior más largo que el inferior, de 1.5–2.2 mm de largo, glabros, de color

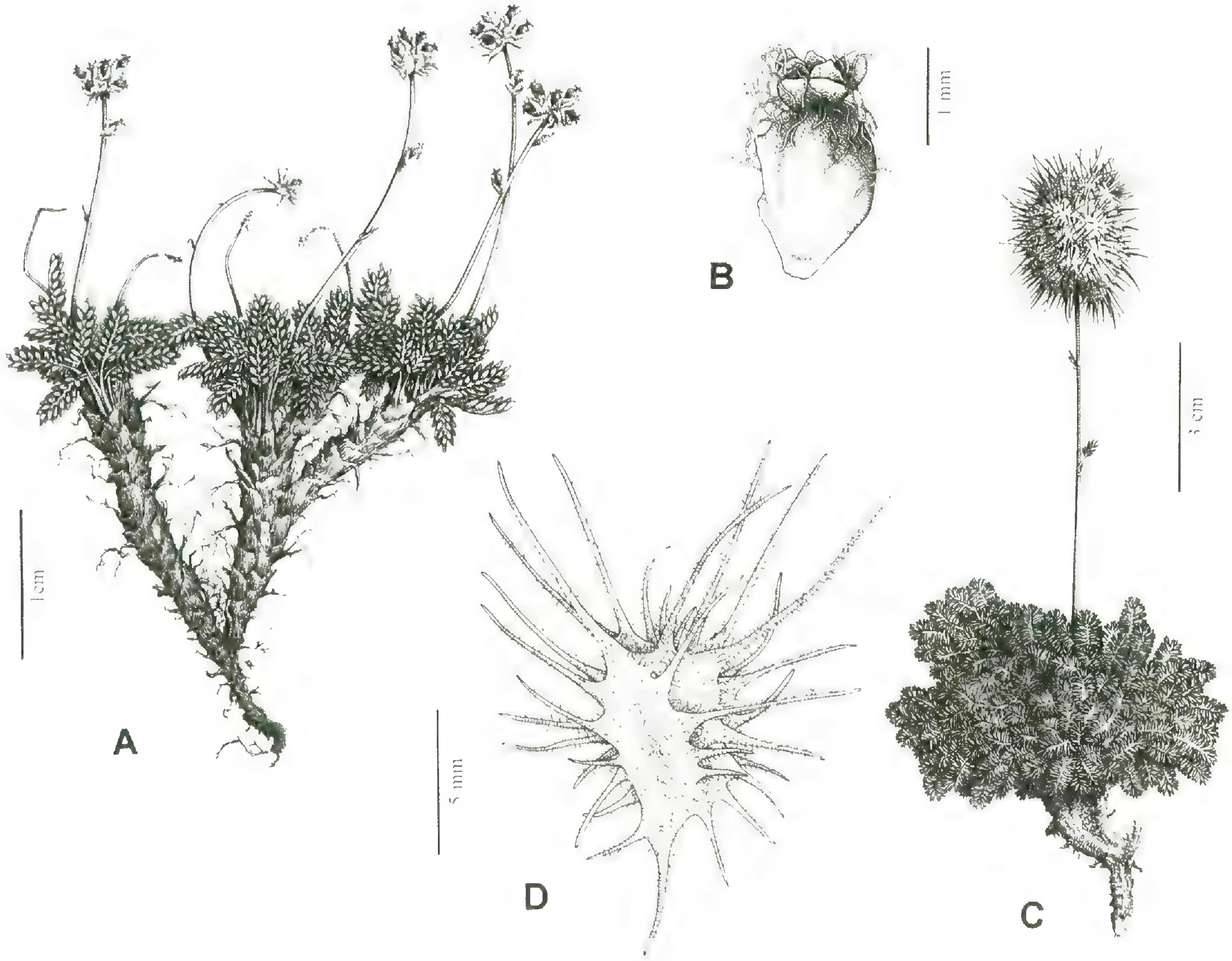

Figura 4. *Acaena lucida.* —A. Hábito. —B. Cupela (*M. T. K. Arroyo 92-393*, CONC). *Acaena macrocephala.* —C. Hábito. —D. Cupela (*Ricardi y Marticorena 5038/1422*, CONC).

verde claro; vainas foliares glabrescentes; apéndices estipulares ausentes. Rama florífera axilar; pedúnculos de 3.3–5 cm de largo, pilosos; inflorescencia capituliforme, de 4.5–5.5 mm de diámetro, con menos de 10 flores, todas acompañadas por brácteas florales ovadas, de ápice agudo, cóncavas, pubescentes en la cara externa y glabras en la interna, de 2–2.5 mm de largo. Sépalos 3–5, ovado-orbiculares, de 0.8–1 mm de largo, pilosos, con un mechón de tricomas en el ápice; estambres 2–3, anteras globosas; estigma globoso, laciniado, ca. 0.3 mm de diámetro. Cupela ovoide, de color morado en la parte superior y amarillo-verdoso en la inferior, de 2–3 mm de largo, con tricomas blancos, blandos, escasos, dispuestos en el tercio superior de la cupela o totalmente pilosa, superficie rugosa; espinas rudimentarias en la parte superior o sin ellas; aquenio 1.

Icones. Grondona, 1964: fig. 22–24; 1984: fig. 451.

Fenología. Fructifica de diciembre (*Elvebakk 538*) a marzo (*Elvebakk 470*).

Distribución y hábitat. Plantita nativa, bastante escasa que crece en laderas rocosas, formando pequeñas champas, en sitios con buen drenaje de la turbera. Se encuentra en la XII Región, desde los 10 a 1100 m de altitud (Fig. 11D). También crece en las Islas Falkland (Moore, 1968) y en Argentina.

Caracteres distintivos. Cupelas sin espinas o muy rudimentarias; sépalos persistentes; folíolos bisectados, los segmentos de distinto largo.

Acaena lucida es el único representante de la Sección *Pleurocephala.* Esta especie es fácilmente reconocible debido a que sus cupelas no poseen espinas, o sólo algunas prominencias hacia el ápice. Aiton (1789) y Lamarck en Lamarck y Poiret (1791) describen independiente *Ancistrum lucidum* basado en una colección proveniente de las Islas Falklands. Lamarck (Lamarck y Poiret, 1791) no se refiere a Aiton, quizás porque su trabajo ya estaba en prensa cuando el vió el de Aiton (Gandhi com. pers.). Luego Vahl (1804) la combina a *Acaena*, y se refiere tanto a Aiton como Lamarck y Poiret (Lamarck y Poiret, 1791), en ese orden. Sin embargo, *Ancistrum lucidum* Lam. es un nombre inválido por ser un homónimo posterior, y la

combinación correcta es la de Aiton por ser el basiónimo más antiguo. Aiton depositó materiales en BM y G-DC, pero no se encontraron. Se estudió un material de Green Plant Herbarium (TRT), perteneciente al Scrapbook de Adam White, que tiene tres plantas, una etiqueta que dice *A. lucida*, Falkland, y se presume es de J. D. Hooker. Sin embargo, el material elegido como neotipo se encuentra depositado en G, y es una carpeta con ocho plantas, la que además fue usada para la ilustración que aparece en *The Botany of the Antarctic Voyage* (Hooker, 1844–1847, pl. 94).

Respecto de los materiales citados para *Acaena lucida* (Lam.) Vahl var. *villosula* Bitter, se pudo examinar tres ejemplares, dos de P, y uno en CONC. Se eligió como lectotipo el espécimen P-106290, que tiene nueve plantas, cinco de las cuales se encuentran en estado reproductivo. El material P-106291 tiene tres plantas, dos en estado reproductivo, en tanto el ejemplar de CONC presenta tres plantas, una en estado reproductivo.

Material representativo examinado. CHILE. **XII Región**: Ultima Esperanza, Senos de Catherine, *Arroyo 92–393* (CONC); P. N. Torres del Paine, 1 km N Salto Grande, *Elvebakk 538* (CONC); P. N. Torres del Paine, 1.5 km SW Refugio Pehoé, *Elvebakk 470* (CONC); Tierra del Fuego, Springhill a Bahía Felipe, 19 Mar. 1955, *Claro de la Maza s.n.* (SGO). ISLAS FALKLAND: *Skottsberg 24* (SGO).

8. Acaena macrocephala Poepp., Fragm. Syn. Pl. 25. 1833. TIPO: Chile: "Cr. in Chile austral. rupibus basalticis ad pedem montis ignivomi Antucensis," *Poeppig 45* (lectotipo, aquí designado, M, foto en CONC!). Figura 4C, D.

Planta hasta 24 cm de alto; tallo totalmente cubierto por las vainas foliares; entrenudos cortos. Hojas sésiles, de 1.4–4.5 cm de largo; lámina en contorno ovado-oblonga; 5–10 pares de folíolos ovados, que se pliegan a lo largo y se disponen uno sobre otro, de 3–6 mm de largo, el margen pinnatisecto, 3 pares de segmentos, cubiertos por tricomas de color amarillo pálido; vainas foliares muy imbricadas, con tricomas largos por todo el margen y el dorso; apéndices estipulares rudimentarios, hasta 2.5 mm. Rama florífera terminal; pedúnculo hasta 11 cm de largo, pubescente, con tricomas largos delgados; inflorescencia capituliforme o raramente subespiciforme, de 1.3–4.5 cm de largo; brácteas basales pubescentes, con un mechón de tricomas en el ápice, de 1.8–3 mm de largo. Sépalos 4, ovado-lanceolados, espatulados, de 2.5–3 mm de largo, pubescentes en el dorso, con un mechón de tricomas blancos en el ápice; estambres 3–5, filamentos ca. 1.5 mm de largo, anteras globosas, moradas, de 0.5–0.6 mm de largo; estigma globoso, de 0.5–1 mm de largo. Cupela ovoide, de 1–1.2 cm de largo, con la epidermis desprendiéndose, velloso-tomentosa, cubierta por espinas blandas, de tamaño similar, pilosas con tricomas largos y finos casi hasta el ápice glabro y sin gloquidios, la base ensanchada o dilatada; aquenio 1.

Icones. Grondona, 1964: fig. 32; 1984: fig. 448.

Fenología. Fructifica de enero (*Ricardi & C. Marticorena 5709*) a marzo (*C. Marticorena et al. 107*).

Distribución y hábitat. Especie nativa, habita en terreno arenoso y rocoso, desde el Descabezado del Maule (Talca, VII Región) a Valdivia, volcán El Mocho (X Región), entre altitudes de 900 a 2500 m (Fig. 11D). También en Argentina.

Caracteres distintivos. Inflorescencia capituliforme grande; espinas de la cupela pilosas a todo largo, con pelos largo y suaves; folíolos pinnatisectos; apéndices estipulares rudimentarios o ausentes.

Acaena macrocephala pertenece a la Sección *Acaena*. Es una especie muy cercana a *A. leptacantha*, de la cual se puede diferenciar sólo en estado fructífero por sus espinas con tricomas blancos y finos, con el ápice glabro, y por la forma de la inflorescencia o infrutescencia que es capituliforme. Bitter (1910) creó la subsección *Asthenoglochinae* donde incluyó a ambas especies. Presenta una distribución bastante restringida, siendo además relativamente escasa. El material tipo de *A. macrocephala* son dos carpetas de *Poeppig 45* depositadas en M y B (fotos 19315 y 3380 respectivamente en CONC). El espécimen de B presumiblemente ha sido destruido, por lo tanto se eligió el de M como lectotipo. La carpeta posee dos plantas, una de las cuales presenta una cabezuela bien desarrollada, característica de la especie. Bitter (1910) describió la variedad *caput-medusae* utilizando los tipos de *A. macrocephala*, por lo tanto dicha variedad es un nombre inválido. Bitter (1910) creó la variedad *intermedia* Bitter considerando que presenta un tamaño intermedio entre la variedad *caput-medusae* y *A. leptacantha*. El protólogo señala el material tipo para B, pero se presume que ha sido destruido. Sin embargo, la foto que aparece en su revisión (tab. 15c), muestra claramente que las características de la variedad caen dentro de la variación natural de la especie.

Material representativo examinado. CHILE. **VII Región**: Talca, Paso Pehuenches, *C. Marticorena et al. 107* (CONC); Laguna del Maule, *A. Marticorena et al. 228* (CONC). **VIII Región**: Ñuble, Termas de Chillán, 3 Feb. 1972, *Duek & Inostroza s.n.* (CONC); Biobío, Faldeos del Volcán Antuco, Laguna de la Laja, *Ricardi & C. Marticorena 5709* (CONC). **IX Región**: Malleco, Termas de Manzanares-Lonquimay, km

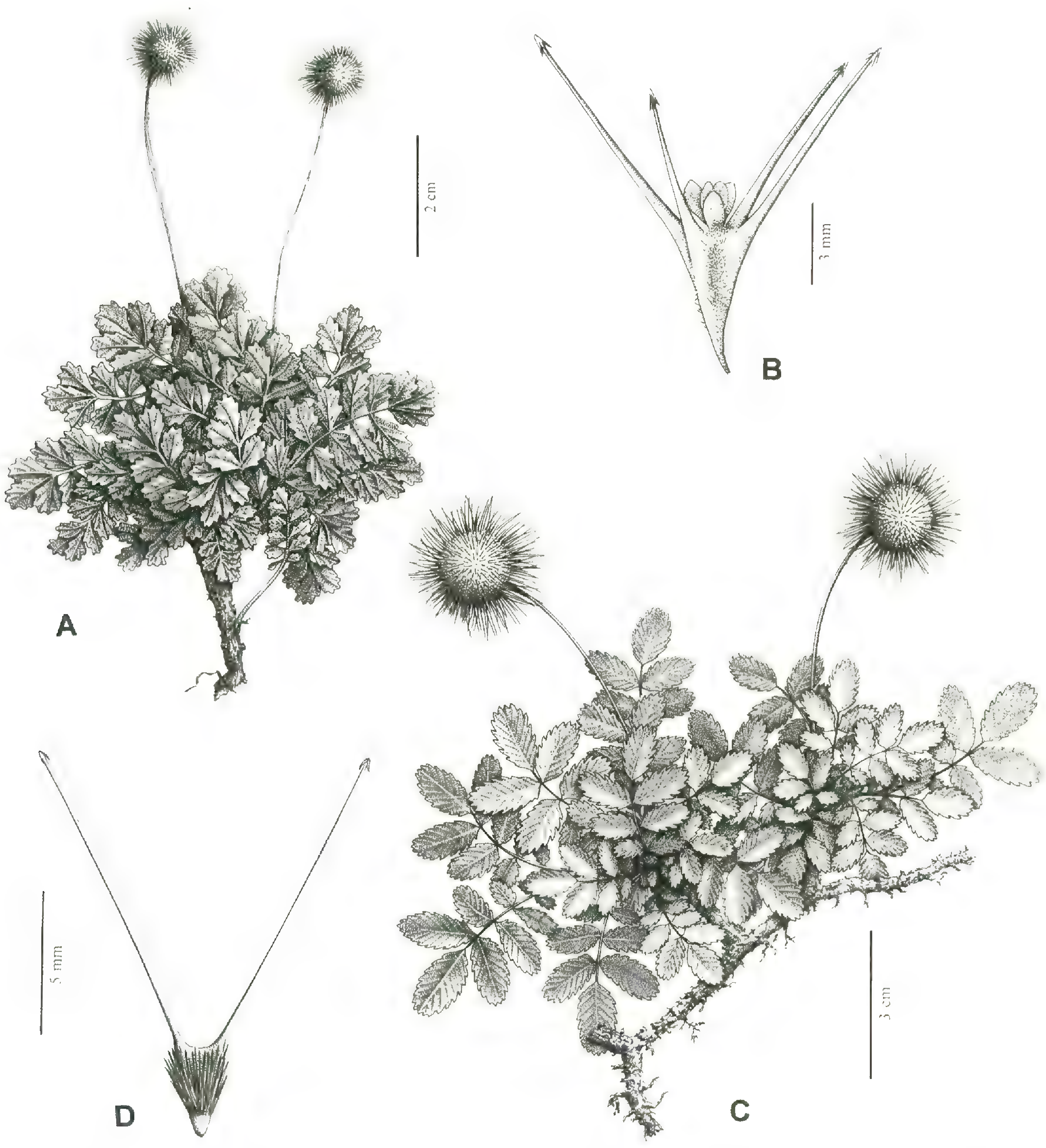

Figura 5. *Acaena magellanica.* —A. Hábito. —B. Cupela (*C. Marticorena et al. 429*, CONC). *Acaena ovalifolia.* —C. Hábito. —D. Cupela (*C. Marticorena et al. 423*, CONC).

29, *Ricardi & C. Marticorena 5014* (CONC); Pino Hachado, 10 Ene. 1948, *Pfister s.n.* (CONC). **X Región**: Valdivia, Volcán El Mocho, 1 Feb. 1953, *Pinto s.n.* (CONC).

9. Acaena magellanica (Lam.) Vahl, Enum. Pl. 1: 297. 1801. *Ancistrum magellanicum* Lam., Illustr. 1. p. 76, tab. 22, fig. 2. 1791. TIPO: Chile. "E. Magellania. Commers. Ex herbario Jussiaei," *Catal. 14218* (lectotipo, aquí designado, P, foto 34722 en CONC!). Figura 5A, B.

Acaena macrostemon Hook. f., Fl. Antarct. 1: 269. 1846. TIPO: Chile. "Hab. Cordillera of Chili, Herb. Cuming 223," *Bridges 522* (lectotipo, aquí designado, K, foto 1244 en SGO!).

Acaena cadilla Hook. f., Fl. Antarct. 1: 269. 1846. TIPO: Chile. "Hab. fields near Valdivia," *Bridges 772* (lectotipo, aquí designado, K, foto 1235 en SGO!).

Acaena closiana Gay, Hist. Chile, Bot. 2. 298. 1847. *Acaena macrostemon* subsp. *closiana* (Gay) Bitter, Biblioth. Bot. 17(74): 193. 1910. TIPO: Chile. "...en las cordilleras de la provincia de Coquimbo, a lo largo de los riachuelos, y a la altura de 6,000 a 10,000 pies;..." *Gay s.n.* (neotipo, aquí designado, P-106316!).

Acaena venulosa Griseb., Syst. Bemerk. 30. 1854. *Acaena laevigata* W. T. Aiton var. *venulosa* (Griseb.) Reiche, Anales Univ. Chile 98: 171. 1897. *Acaena magellanica*

subsp. *venulosa* (Griseb.) Bitter, Biblioth. Bot. 17(74): 168. 1910. TIPO: Chile. "Penins. Brunswick: in collibus pr. Sandy Point, m. Octobri," *Lechler 978c* (lectotipo, aquí designado, M!).

Acaena canescens Phil., Reise Atacama: 192. 1860. TIPO: Chile. "In partis meridionalis deserti Atacamensis vallibus editioribus rara non est, e.g. Cachinal de la Sierra, 7000 p.s.m., Sandon 9000 p.s.m.," *Philippi 596a* (lectotipo, aquí designado, SGO-39729!; duplicados, SGO-49883!).

Acaena coxi Phil., Linnaea 33: 63. 1864. TIPO: Chile. "Pariter de planitie patagonica ad radicem Andinum Valdivianarum. año 1803," *G. Cox s.n.* (holotipo, SGO-49832!).

Acaena krausei Phil., Anales Univ. Chile 41: 711. 1872. TIPO: Chile. "Común en la provincia de Valdivia, señaladamente cerca del Corral, Ene. 1838," *Philippi s.n.* (lectotipo, aquí designado, SGO-49934!).

Acaena hirsuta Phil., Anales Univ. Chile 41: 712. 1872. *Acaena krausei* var. *hirsuta* (Phil.) Reiche, Anales Univ. Chile 98: 170. 1897. TIPO: Chile. "De la provincia de Valdivia; común en mi fundo de San Juan, Feb. 1858." *Philippi s.n.* (lectotipo, aquí designado, SGO-49858!).

Acaena petiolulata Phil., Anales Univ. Chile 84: 624. 1893. TIPO: Chile. "In Andibus provinciae Santiago loco Valle del Yeso, Ene. 1866," *Philippi 559* (lectotipo, aquí designado, SGO-39723!; duplicados, SGO-49885!)

Acaena hirta Citerne, Rev. Sci. Nat. Ouest 7(2): 43. 1897. TIPO: "Chile austral.," colector desconocido (neotipo, aquí designado, P, foto 34719 en CONC!).

Acaena longiaristata H. Ross, Oesterr. Bot. Z. 57: 449. 1907. *Acaena macrostemon* Hook. f. subsp. *longiaristata* (H. Ross) Bitter, Biblioth. Bot. 17(74): 192. 1910. TIPO: Chile. "Uspallata-Paβ der chilenischen Hochcordillere (36° südl. Breite): Juncal, 2300 m, 7.II. 1903, in Baenitz, herb. Americ. Nr. 1263," *O. Buchtien s.n.* (lectotipo, aquí designado, BREM!; duplicado, WRSL!).

Acaena glaucella Bitter, Biblioth. Bot. 17(74): 157. 1910. TIPO: Chile. "Punta Arenas, 16 Dic. 1895," *Dusén 188* (isotipo, UPS no visto, sinonimia según Walton, 1975).

Acaena macropoda Bitter, Biblioth. Bot. 17(74): 159. 1910. TIPO: Chile. "Patagonia australis: Cerro Toro, Svensk. exp. Patag. 18 Mar. 1899, sub nom. *A. laevigata* Aiton," *O. Borge 214* (holotipo, S-8053!).

Acaena magellanica var. *glabrescens* Bitter, Biblioth. Bot. 17(74): 168. 1910. TIPO: Chile. "Penins. Brunswick: in collibus pr. Sandy Point, m. Octobri," *Lechler 978c* (lectotipo, aquí designado, BREM!)

Acaena magellanica subsp. *pygmaea* Bitter, Biblioth. Bot. 17(74): 169. 1910. TIPO: Chile. "Cord. de Maule, sub nom. *A. laevigata* Aiton, ann. 1856–1857," *Ph. Germain s.n.* (lectotipo, aquí designado, W-359414!).

Acaena obtusiloba Bitter, Biblioth. Bot. 17(74): 182. 1910. TIPO: Chile. "Regio Magellanica: Cape Gregory Bay, Straights [sic] of Magellan," *Capt. King 16* (holotipo, G, foto 27426 en CONC!).

Acaena neglecta Bitter, Biblioth. Bot. 17(74): 183. 1910. TIPO: Chile. "Magellansland, N.J. (1852), sub nom. *A. adscendens* Vahl," *Andersson 280* (lectotipo, aquí designado, S-8058!).

Acaena longistipula Bitter, Biblioth. Bot. 17(74): 204. 1910. TIPO: Chile. "Cord. de Linares, in herb. Stockh. sub nom. *A. canescens* Phil.," *Germain s.n.* (holotipo, S-8049!).

Acaena macrostemon Hook. f. var. *basipilosa* Bitter, Biblioth. Bot. 17(74): 193. 1910. TIPO: Chile. "Uspallata-Paβ der chilenischen Hochcordillere (36° südl. Breite): Juncal, 2300 m; 7.II. 1903," *O. Buchtien 5464* (lectotipo, aquí designado, M!).

Acaena colchaguensis Bitter, Biblioth. Bot. 17(74): 205. 1910. TIPO: Chile. "Cordillera de Colchagua, sub nom. *A. canescens* Phil. Herb. Berol.," *Philippi s.n.* (isotipo, FI, no visto, sinonimia según Walton, 1975).

Acaena depauperata Bitter, Biblioth. Bot. 17(74): 206. 1910. TIPO: Chile. "Cordillera de Maule, unâ cum spec. 81 *A. grandistipula* Bitt. sub nom. *A. deserticola* Phil.," *Ph. Germain 88b* (holotipo, FI, no visto, sinonimia según Walton, 1975).

Acaena humilis Bitter, Biblioth. Bot. 17(74): 206. 1910. TIPO: Chile. "Andes de Santiago, herb. Monac.," *F. W. Neger s.n.* (holotipo, M!).

Acaena grandistipula Bitter, Biblioth. Bot. 17(74): 206. 1910. TIPO: Chile. "Cordillera de Maule, sub nom. *A. deserticola* Phil.," *Ph. Germain s.n.* (lectotipo, aquí designado, K, foto 1241 en SGO!; duplicado, FI, no visto).

Acaena ischnostemon Bitter, Biblioth. Bot. 17(74): 210. 1910. TIPO: Chile. "Hab: 'Magallanes, sub nom. *A. laevigata?* Aiton'," *Philippi s.n.* (lectotipo, aquí designado, W-116067!).

Acaena grossifolia Bitter, Biblioth. Bot. 17(74): 211. 1910. TIPO: Chile. "Patagonia australis: Cape Fairweather (Buentiempo), herb. Delessert," *Capt. King 10* (holotipo, G, foto 27424 en CONC!).

Acaena macrophyes Bitter, Biblioth. Bot. 17(74): 212: 1910. TIPO: Chile. "Distributio: Regio magellanica: Orange Bay (Hoste Isl.) Mission du Cap Horn 1882–83, herb. Paris," *Hyades 901* (holotipo, P-106312!).

Acaena krausei Phil. var. *massonandra* Bitter, Biblioth. Bot. 17(74): 222. 1910. TIPO: Chile. "Circa Valdivia et Osorno, herb. Webbianum in herb. Florent.," *Bridges 773* (holotipo, FI, no visto; isotipo, CONC-29693!).

Acaena krausei Phil. subvar. *glabratula* Bitter, Biblioth. Bot. 17(74): 223. 1910. TIPO: Chile. "Chile: Corral, herb. Berol., Brem.," *Ochsenius s.n.* (lectotipo, aquí designado, BREM!).

Acaena glandulifera Bitter, Biblioth. Bot. 17(74): 223. 1910. TIPO: Chile. "Patagonia occidentalis: In valle fluminis Aysén, sub nom. *A. adscendens* Vahl, 14.1.1897 florentem et fructiferam herb. Stockh., Upsal.," *Dusén s.n.* (lectotipo, aquí designado, S-R8044!).

Acaena subflaccida Bitter, Biblioth. Bot. 17(74): 225. 1910. TIPO: Chile. "Patagonia australis: Punta Arenas, Plantae in reg. Magell. lectae sub nom. *A. adscendens* Vahl, herb. Upsal.," *Dusén 190* (holotipo, UPS, no visto, sinonimia según Walton, 1975).

Acaena rubescens Bitter, Biblioth. Bot. 17(74): 225. 1910. TIPO: Chile. "Patagonia australis: Punta Arenas, Rio de las Minas, cum fructibus submaturis unâ cum *A. exaltata* Bitt., exped. suec. 1907–1909, 20.2.1908," *Skottsberg 175* (holotipo, SGO-58846!).

Acaena oligoglochin Bitter, Biblioth. Bot. 17(74): 227. 1910. TIPO: Chile. "Punta Arenas. Terrains secs pelouses, Expéd. de la Magicienne fructigera sub nom. *A. adscendens* Vahl var. *macrochaeta* Franch, herb. Mus. Paris, 10 Feb. 1877," *Savatier s.n.* (holotipo, P-106309!).

Acaena exaltata Bitter, Biblioth. Bot. 17(74): 229. tab. 24. 1910. TIPO: Chile. "Patagonia australis: Punta Arenas, Rio de las Minas, cum fructibus submaturi, unâ cum *A. rubescens* Bitt., exped. suec. 1907–09, 20.2.1908,"

Skottsberg s.n. (isotipo, UPS, no visto, sinonimia según Walton, 1975).

Acaena plioglochin Bitter, Biblioth. Bot. 17(74): 230. 1910. TIPO: Chile. "Fretum magellanicum: Peninsula Brunswick, Port Famine, unâ cum specimine *A. ovalifolia* R. et P. sine nomine in herb. Delessert," *Capt. King 46* (holotipo, G, foto 27428 en CONC!).

Acaena brachyglochin Bitter, Biblioth. Bot. 17(74): 291. 1910. TIPO: Chile. "In cordillera at 3500 ped., pl. chilensis 129," *Philippi s.n.* (holotipo, BREM, no visto, sinonimia según Walton, 1975).

Planta hasta 25 cm de alto; rizoma ca. 5.5 mm de diámetro; tallo glabro, ascendente; entrenudos cortos. Hojas en contorno oblongas a linear-lanceoladas, de 2.2–12.5 cm de largo; 5–10 pares de folíolos, obovados, base cuneada, de 6–33 mm de largo, el margen pinnatipartido, 4–7 pares de segmentos, glabros a pubescentes, con tricomas cortos, delgados, blancos a transparentes, más abundantes en el envés; vainas foliares presentes, apéndices estipulares lanceolados, de 3–5 mm de largo, el margen irregular, glabrescentes. Rama florífera terminal; pedúnculo hasta 20 cm de largo, glabro a pubescente; inflorescencia capituliforme, morada o amarilla, hasta 15 mm de diámetro; brácteas basales alargadas, de forma irregular, hasta 6 mm de largo; algunas flores encontrándose a lo largo del pedúnculo floral, cercanas al ápice. Flor hermafrodita con sépalos 4–5, ovado-elípticos, de 0.8–2.6 mm de largo, cara interna glabra, brillante, cara externa pubescente con tricomas transparentes, largos; estambres 2–5, filamentos de 2–3.5 mm de largo, anteras globosas a lanceoloides, moradas, de 1.2–2 mm de largo; estilo corto, estigma obovoide a lanceoloide, laciniado, amarillo a morado, 1–2.5 mm de largo. Flor femenina con estigmas notorios, 3 mm de largo, estaminodios 0.5–1 mm de largo. Cupela obcónica, tetrágona, de 1–6 mm de largo, pilosa con tricomas blandos, persistentes, blancos, con 4 espinas apicales, de base angosta, raro 3 ó 5, desiguales, hasta 10 mm, con fuertes gloquidios; aquenios 1.

Icones. Grondona, 1964: fig. 11–13; 1984: fig. 446.

Fenología. Fructifica de diciembre (*A. Marticorena et al. 98*) a junio (*Loyola & Morales 1*).

Se observaron flores femeninas (*Arancio & Squeo 10296, Ricardi 2900, Squeo 88068*), y también algunas con características masculinas (*Zoellner 6793, Rodríguez 3184, Rodríguez y Ruiz 3715*).

Distribución y hábitat. Especie nativa, crece en suelos arenosos húmedos, en vegas, en grietas de rocas, a orillas del agua. Se distribuye ampliamente desde la I Región (Arica, Puquios) hasta la XII Región (Caleta Misión, Isla Hoste), del nivel del mar hasta 4200 m de altitud (Fig. 11E). Presenta una amplia distribución la que comprende el sur de Sudamérica, y las Islas Kerguelen, Islas Marion, Islas South Georgia, Islas Macquarie e Islas Falkland (Greene, 1964; Moore, 1968; Walton, 1979; Pisano, 1984). Sin embargo, es interesante señalar la ausencia de esta especie en el Archipiélago de Juan Fernández, donde si crece abundantemente *Acaena argentea*, y en menor cantidad *A. ovalifolia* (Marticorena & Cavieres, 2000).

Nombre común. Amor seco (*Montero 12650*), cadilla (Baeza, 1921), trun (*Aravena 29*).

Caracteres distintivos. Cupela obcónica-tetrágona, con 4 espinas apicales glabras a algo pilosas; capítulo maduro verdoso, de hasta 15 mm de diámetro.

Acaena magellanica pertenece a la Sección *Ancistrum*. Grondona (1964) y Greene (1964) señalan a *A. adscendens* Vahl (1804) como sinónimo de *A. magellanica*, sin embargo no se ha conseguido localizar o ver el tipo, por lo tanto no se ha podido confirmar la sinonimia. Para el sinónimo *A. closiana* Gay (1847), no fue posible localizar el material tipo, por lo tanto se eligió un neotipo de un material cuyos datos se corresponden con los originales, excepto por el año 1858, pues la especie fue descrita en 1847.

Para *Acaena macrostemon*, estudié un fotografía del material tipo (K), y las características generales pertenecen a *A. magellanica*, cuya descripción original dice "...calycis aristis 2 caeteris duplo longioribus...," y establezco que esto se refiere a que posee dos espinas del doble del largo de las otras, es decir son cuatro, lo que se corresponde con *A. magellanica*.

Se ha estudiado material de *Lechler 978c*, uno proveniente de M, con el que están relacionados los nombres *Acaena venulosa*, *A. laevigata* var. *venulosa*, *A. magellanica* subsp. *venulosa*, y uno de BREM asociado a *A. magellanica* var. *glabrescens*. El material de M fue asignado como tipo del epíteto *venulosa*, y el material de BREM como tipo a *glabrescens*.

En SGO se encuentran dos materiales con los datos de localidad, el N 39729 presenta una planta con la inflorescencia inmadura, cuya etiqueta dice *Acaena canescens* y el nombre *deserticola* rayado, el N 49883 tiene una planta sin inflorescencia, con una etiqueta con el nombre *A. deserticola* Phil., y con datos de localidad más completos, pero esta no fue publicada, luego se designó como lectotipo N 39729 por ser una planta más completa. Para el nombre *A. krausei*, el material SGO-49934 presenta tres etiquetas, de las cuales una corresponde con el protólogo de la especie, es una planta completa con frutos maduros. Para *A. hirsuta* se encontraron dos materiales en SGO, pero uno correspondía con la fecha de recolección feb. 1858, y fue elegido con lectotipo. Dos materiales se estudiaron para *A.*

petiolulata, ambos provenientes de SGO, uno estéril (SGO-39723) y el otro fértil (SGO-49885) que fue elegido como lectotipo.

Se estudiaron dos materiales de *Acaena longiaristata*, de BREM y WRSL, pero se eligió el de BREM por presentar dos plantas con inflorescencias, en tanto la planta de WRSL es infértil. Bitter (1910) menciona de modo general, materiales de *A. macrostemon* var. *basipilosa* depositados en M, de los cuales se estudiaron dos, pero no son duplicados, ya tienen números de colector distintos (5410 y 5464), y se eligió el N°5464 por presentar dos plantas bien desarrolladas y tres hojas extendidas. Para *A. magellanica* subsp. *pygmaea*, se citaron dos materiales, ambos de W, pero uno colectado por Philippi en la Cordillera de Linares, y el otro de Germain en la Cordillera de Maule. Ambos fueron estudiados y se eligió el N° 359414 de Germain, que presenta dos plantas fértiles. Bitter (1910) menciona dos materiales para *A. neglecta*, en UPS y S, pero sólo se pudo estudiar el de S-8058, que presenta dos plantas, una fértil, y fue elegida como tipo. Para *A. ischnostemon* menciona materiales para B y W, pero sólo se pudo estudiar dos materiales de W, y se eligió el que presenta tres inflorescencias, con el N° 31361 en una reglilla, y como duplicado W-116067. Para *A. krausei* subvar. *glabratula*, Bitter (1910) menciona materiales para B, y BREM, sólo se pudo estudiar el material de BREM, que corresponde a dos plantas bien desarrolladas, y que fue elegido como tipo. Para *A. hirta* Citerne se designó un neotipo que corresponde a un material de Gay (N° 71), depositado en P, debido a que no se encontró el material original.

Entre los taxa descritos por Bitter (1910), muchos fueron basados en caracteres variables dentro de la especie. Se pueden mencionar 22 especies, 5 subespecies, 5 variedades y 2 subvariedades; por ejemplo: folíolos blanquecinos (*Acaena glaucophylla* Bitter), brácteas notorias entre las flores (*A. frondosibracteata* Bitter), escaso número de dientes en los folíolos (*A. oligodonta* Bitter), folíolos inferiores lobulados (*A. obtusiloba*), número de gloquidios (*A. triglochin* Bitter), largo de los sépalos (*A. longisepala* Bitter), número de dientes del folíolo (*A. novemdentata* Bitter), y así la lista continua.

Los materiales tipo que fueron depositados en Berlín, fueron destruidos durante la Segunda Guerra Mundial. Dentro de estos he podido ver fotos del tipo de *Acaena triglochin*, *A. longisepala*, *A. novemdentata*, *A. molliuscula*, *A. acutifida* Bitter y *A. stellaris* Meyen, los que sin duda por sus características corresponden a *A. magellanica*. Sin embargo, para otros no se encontró material fotográfico, como *A. purpureistigma* Bitter, *A. krausei* Phil. subvar. *pilosior* Bitter, *A. frondosibracteata* y *A. oligoglochin* Bitter var. *dolichoglochin* Bitter. A pesar de esto, dichos taxa son reconocibles con *A. magellanica*, de acuerdo a la detallada descripción que hace Bitter (1910), pero no se pudo localizar material relacionado. Otra situación se presenta con taxa donde no se mencionó material tipo. Para algunos fue posible determinarlos como *A. magellanica*, debido a que Bitter (1910) en su revisión incluyó fotos de algunos taxa, como para *A. basibullata* Bitter (tab. 23). Kalela (1940), describió *A. subnitens* Kalela de cinco materiales provenientes de Magallanes, pero no señaló herbario. En el artículo realizó una completa descripción, que concuerda con *A. magellanica*, lo que se corrobora al examinar las dos fotos (tab. 14, 15) que en él aparecen, y con lo cual Grondona (1964) también concordó. Por último, para algunos taxa no fue posible localizar material tipo, principalmente porque no fue señalado, aunque las descripciones permitieron reconocerlas como *A. magellanica*. Dentro de estas podemos mencionar *A. denudata* Reiche, a la que Walton (1975) señala como su sinónimo. *Acaena laevigata*, según señala Grondona (1964), fue considerada por W. T. Aiton (1810–1813) lo que Lamarck (Lamarck y Poiret, 1791–1823) describieron como *Ancistrum magellanicum* var. β, la que probablemente sólo corresponde a *Acaena magellanica*. Un caso distinto es el de *Acaena glandulifera* Bitter subsp. *nordenskjoeldii* Bitter, donde tampoco se localizó material original, pero que además su descripción parece haber sido hecha desde un material algo inmaduro, debido al diámetro de la inflorescencia, y al tamaño de las espinas de la cupela. No obstante, en términos generales es bastante similar a *A. magellanica*.

Respecto de su número cromosómico, se ha determinado la presencia de poblaciones diploides con un $2n = 42$, y tetraploides con $2n = 84$, las que se encuentran en islas subantárticas, y en el sur de Chile e Islas Falkland respectivamente (Moore & Walton, 1970). Estas diferencias parecen tener relación con las glaciaciones del Pleistoceno, donde hubo dispersión luego que los hielos se retiraron colonizando zonas boscosas del sur (Moore, 1972; Roulet, 1981). Se sabe que esta especie sólo hibridiza con *Acaena tenera*, y que esta falta de hibridación con otras especies se deba a que la mayoría de sus poblaciones en Sudamérica son probablemente tetraploides (Walton, 1979).

En relación a su sistema reproductivo, es una especie ginodioica (Arroyo & Squeo, 1989), aunque es posible encontrar algunas plantas con caracteres predominantemente masculinos, con grandes anteras y estigmas pequeños, pero no se conoce si son o no funcionales (Walton, 1979). Su inflorescencia puede variar considerablemente, y puede presentar algunas anormalidades como cupelas pediceladas o más de

cuatro espinas (Walton, 1977, 1979). Esta variabilidad provocó que se describieran muchos taxa, como es el caso de Bitter (1910) y Philippi (1862, 1863, 1872, 1893), algunos de los cuales fueron posteriormente pasados a sinonímia (Grondona, 1964; Walton, 1975). Esta especie corresponde claramente a un complejo y es probable que existan divisiones infraespecíficas reconocibles.

Material representativo examinado. ARGENTINA. **Sta. Cruz**: Güer Aike, Est. Las Viscachas, *T.B.P.A. 2537* (HIP); Río Gallegos, *T.B.P.A. 223* (HIP); Est. Sofía, *T.B.P.A. 3142* (HIP). **Tierra del Fuego**: Est. Cullen, *Moore 2603* (HIP); Bahia Thetis, *Goodall 2283* (HIP). CHILE. **I Región**: Arica, Puquios, *Loyola & Morales 4* (CONC). **II Región**: El Loa, Toconao, 7 Ene. 1950, *Pfister s.n.* (CONC); Socaire, *Rodríguez 3184* (CONC); Quebrada de Socaire, *Rodríguez & Ruiz 3715* (CONC); Antofagasta, Vega Aguada de Choscha, *Arroyo & Villagrán 831286* (CONC); Quebrada del Chaco, *Arancio & Squeo 10296* (CONC). **III Región**: Chañaral, Camino de Potrerillos a Salar de Maricunga, *Ricardi et al. 1632* (CONC); Copiapo, Cam. Internac. a Tinogasta, Cuesta del Colorado, *Ricardi et al. 1662* (CONC); Huasco, Acerillos, Desierto de Atacama, 15 Nov. 1977, *Villanueva s.n.* (SGO); Río del Estrecho, *Arancio et al. 91201* (CONC). **IV Región**: Elqui, Baños del Toro, *Ricardi et al. 693* (CONC); El Indio, *Squeo 88068* (CONC); Limarí, Embalse de La Laguna, *Ricardi et al. 722* (CONC); Choapa, Hierba Loca, *Jiles 4215* (CONC). **V Región**: Los Andes, Caracoles, *Ricardi 2900* (CONC); Riecillo, *Zoellner 6793* (CONC). **Región Metropolitana**: Santiago, Potrero Grande, *Zoellner 1474* (CONC); Cordillera, Baños Morales, *A. Marticorena et al. 98* (CONC). **VI Región**: Cachapoal, Sewell, *Pennell 12333* (SGO); Colchagua, Termas del Flaco, 15 Feb. 1986, *Nuñez & Labra s.n.* (SGO). **VII Región**: Curicó, Paso Vergara, *C. Marticorena & Matthei 1007* (CONC); Talca, Entre Laguna del Maule y Paso Pehuenches, *Ricardi et al. 966* (CONC); Linares, Cordillera de Linares, *F. Philippi s.n.* (SGO). **VIII Región:** Ñuble, Termas de Chillán, *Beckett et al. 4422* (SGO); Arauco, Cordillera de Nahuelbuta, Pino del Finado, *Quezada 228* (CONC); Biobío, Camino de Ralco a Lepoy, *A. Marticorena et al. 297* (CONC). **IX Región**: Malleco, Entre Angol y P. N. Nahuelbuta, *Taylor et al. 10382* (CONC); Camino Liucura–Pino Hachado, km 19, *Ricardi & C. Marticorena 5063* (CONC); Cautín, Refugio Volcán Llaima, *Ricardi & Matthei 5305* (CONC); Puerto Saavedra, *Aravena 29* (CONC). **X Región**: Valdivia, Panguipulli, cam. Pullinque Coñaripe, *C. Marticorena et al. 429* (CONC); San José, *Montero 12650* (CONC); Osorno, P. N. Puyehue, Refugio Antillanca, *Gardner & Knees 3849* (CONC); Llanquihue, Puerto Montt, Los Alerces, 3 Feb. 1960, *Saa s.n.* (CONC); Chiloé, Isla Doña Sebastiana, *C. Marticorena 1616* (CONC). **XI Región**: Coihaique, Lago Seco, *Schlegel 2318* (CONC); Aisén, Laguna San Rafael, *Muñoz 6099* (SGO); General Carrera, Laguna Fontana, *Braynshaw 246* (HIP); Capitán Prat, Glaciar Bernardo, *Anliot 6140* (SGO). **XII Región:** Ultima Esperanza, Est. La Porfiada, Sierra Baguales, *Pisano & Cárdenas 4644* (HIP); Cerro Donoso, Río de Las Chinas, *Arroyo et al. 870202* (CONC); Torres del Paine, Cerro Diente, *Arroyo & Squeo 860084* (CONC); P. N. Torres del Paine, Laguna Mellizas, *Elvebakk 35* (CONC); Sierra del Toro, *Arroyo et al. 92165* (CONC); Magallanes, Escorial de Pali Aike, *Dollenz 207, 220, 241* (HIP); Pto. Altamirano, Seno Skyring, *Pisano & Henríquez 6782* (HIP); Península Muñoz Gamero, Pto. Ramírez, *Pisano & Dollenz 5765* (HIP); Punta Arenas, Chabunco, 8 Ene. 1952, *Pfister & Ricardi s.n.* (CONC); Tres Brazos, 15 Ene. 1960, *Saa s.n.* (CONC); Bahía Morris, Isla Capitán Aracena, *Pisano 3301* (CONC, HIP); Tierra del Fuego, Punta Espora, *Moore 2369* (HIP); Cuarto Chorrillo, Bahía Lomas, *Pisano 3169* (HIP); Est. Brazo Norte, *Pisano 2552* (HIP); China Creek, Est. Por fin, *Dollenz 297* (HIP); Cordón Baquedano, Sect. Río del Oro, *Pisano & Henríquez 6901* (HIP); Dunas Río Marazzi, *Pisano 3210* (HIP); Bahía Inútil, Est. Cameron, *Moore 1074* (SGO); Antártica Chilena, Fiordo Parry, Punta Canoa, *Pisano 3106* (CONC, HIP); Isla Navarino, Puerto Toro, *Dollenz 440* (HIP); Caleta Awaiakirrh, Isla Hoste, Itsmo, *Pisano 5494, 5521* (HIP); Isla Wollaston, Caleta Lientur, *Pisano 4969* (HIP); Caleta Misión, Isla Hoste, Bahía Orange, 15 Nov. 1975, *Samsing s.n.* (HIP). ISLAS FALKLAND: West F. Fox Island, *Skottsberg 32* (SGO). SOUTH GEORGIA: King Edward Point, *Headland 562* (HIP).

10. Acaena masafuerana Bitter, Biblioth. Bot. 17(74): 45, tab. 2. 1910. TIPO: Chile. "Juan Fernandez: Mas a fuera, una cum *A. ovalifolia* R. et P. var. *insulae-exterioris* Bitt. 1100–1300 m (expedit. suec. 1907–09)," *Skottsberg s.n.* (holotipo, S-R8057!). Figura 6A, B.

Planta hasta 9.5 cm de alto, leñosa en la base; tallo cubierto por las vainas foliares; entrenudos cortos. Hojas de 1–7.5 cm de largo; lámina en contorno obovado-lanceolada; 3–4 pares de folíolos, obovados, asimétricos en la base, 3–7 mm de largo, el margen inciso, con una separación entre par y par mayor que el largo de los folíolos, con tricomas cortos y brillantes, en las nervaduras en ambas caras; vainas foliares glabras; apéndices estipulares de base ensanchada, de 0.5–2 mm. Rama florífera terminal; pedúnculo hasta 9.4 cm de largo, glabro a glabrescente; inflorescencia capituliforme, de 3.5–6.5 mm de diámetro; brácteas basales obovadas, el margen pubescente, de 1–1.5 mm de largo, con tricomas articulados de color anaranjado oscuro, brillantes, entre las brácteas y las cupelas. Sépalos 4, ovados, de 0.9–1.3 mm de largo, glabros, con manchitas de color café rojizo a lo largo; estambres 2, anteras globosas, ca. 0.3 mm de largo; estilo corto, estigma globoso, laciniado, de 0.4–0.6 mm de largo. Cupela ovoide, de 1–2 mm de largo, con tricomas glandulares entre y en la base de las cupelas, 4 espinas cortas de base angosta en el ápice, con fuertes gloquidios; aquenio 1.

Icon. Skottsberg, 1921: 131.

Fenología. Fructifica de enero (*Stuessy & Lammers 9211*) a febrero (*Landero & Ruiz 9592*).

Distribución y hábitat. Especie endémica de la isla Más Afuera del Archipiélago de Juan Fernández (Fig. 12A). Crece en el fondo de las quebradas, entre y sobre rocas, donde se reconoce por sus sépalos amarillo-verdosos y estambres de color violáceo,

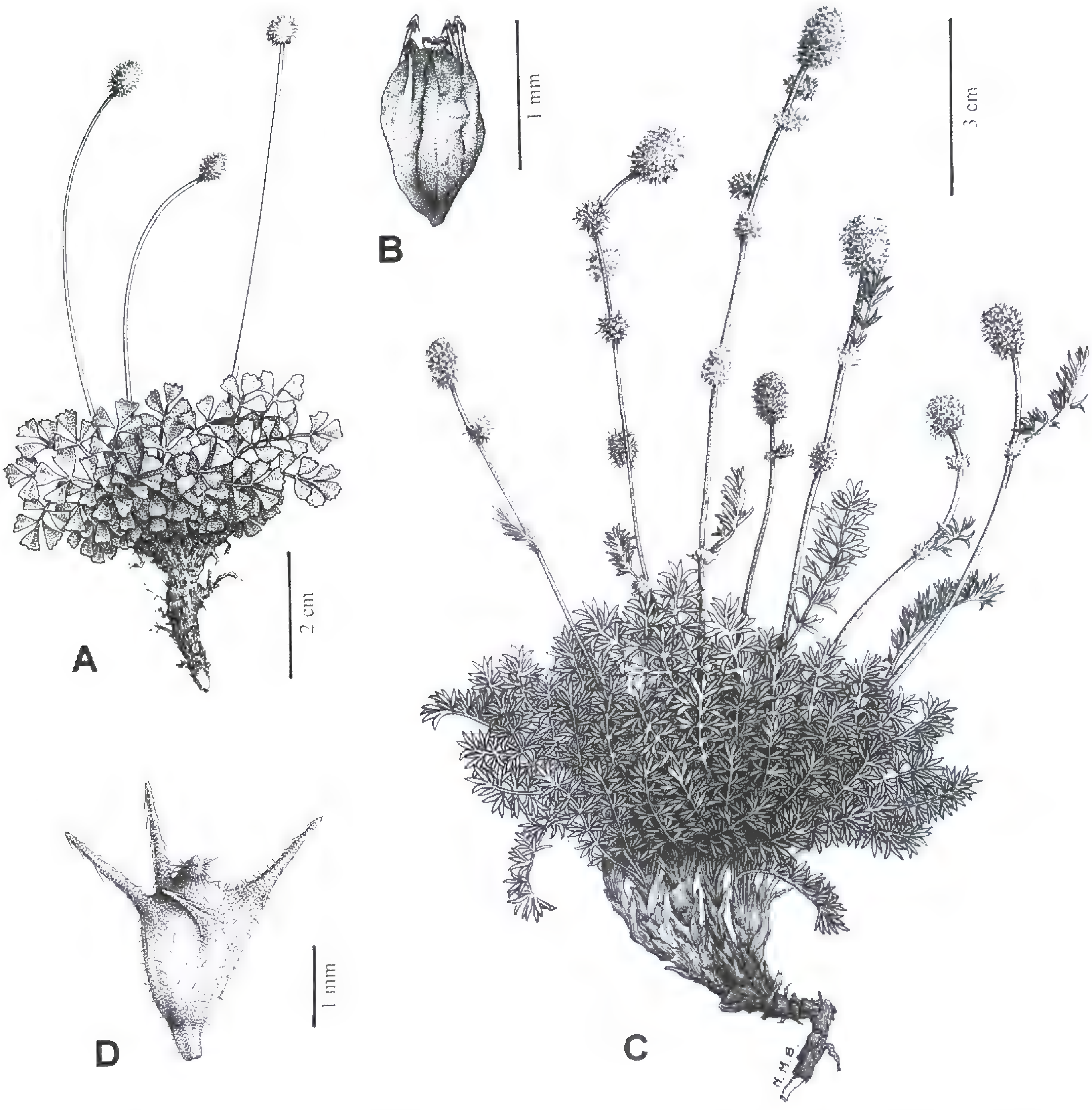

Figura 6. *Acaena masafuerana*. —A. Hábito. —B. Cupela (*Valdebenito y Landero 9030*, CONC). *Acaena patagonica*. —C. Hábito (*Arroyo & Squeo 870189*, CONC). —D. Cupela (*Elvebakk 532*, CONC).

formando cojines, desde los 900 a más de 1300 m de altitud.

Caracteres distintivos. Capítulos de hasta 6.5 mm de diámetro; cupela con 4 espinas apicales más cortas que la mitad del largo de la cupela; folíolos obovados, asimétricos en la base, con tricomas glandulares entre las cupelas.

Acaena masafuerana pertenece a la Sección *Acrobyssinae*. Esta especie es afín a *A. antarctica* en cuanto a su pequeño tamaño, la forma y tamaño de las cupelas, forma de los folíolos, y los tricomas glandulares dispuestos entre las cupelas. La especie fue descrita por Bitter (1910) basado en material incompleto sin flores ni frutos. Al estudiar la cara inferior de las hojas observó que presentaban células papilosas, carácter que también observó en las especies *A. pumila* y *A. exigua*, ambas pertenecientes a la sección *Subtuspapillosae*. También menciona la presencia de estolones, y advierte que las anteriores especies también los poseen. Debido a que sólo contaba con material estéril, y a la similitud anatómica de las tres especies incluyó a *A. masafuerana* dentro de la sección *Subtuspapillosae*. Sin embargo, señala que las células papilosas de *A. pumila* y *A. exigua* están mucho más desarrolladas que las de *A. masafuerana*, y mantiene muchas dudas sobre su inclusión en la sección. Posteriormente, Skottsberg (1921) estudió material fértil, y pudo ver que la especie compartía muchos caracteres con *A. antarctica* y por lo

tanto la ubicó en la sección *Acrobyssinae*. Se observó además que *A. masafuerana* presenta el mismo patrón celular de la cupela (tipo axillares) que *A. antarctica*, *A. tenera*, *A. lucida* y *A. pumila* (Marticorena, 2000).

Material representativo examinado. CHILE. **V Región**: Valparaíso, Juan Fernández, Más Afuera, N Quebrada Casas, *Stuessy & Lammers 9211* (CONC); Quebrada Pastos, *Stuessy & Lammers 9416* (CONC); Cordón La Cuchara, *Valdebenito & Landero 9030* (CONC); Cordón Atravesado, *Stuessy et al. 9365* (CONC); Plano de Rodríguez, *Valdebenito 9132* (CONC); Quebrada El Canelo, *Valdebenito & Landero 6432* (CONC); Entre Quebrada Vacas y Quebrada Guatón, *Stuessy et al. 9323* (CONC); Cerro Inocentes, *Landero & Ruiz 9592* (CONC); Cerro Verde, *Stuessy 9121* (CONC); Quebrada Larga, *Stuessy & Ruiz 9448* (CONC).

11. **Acaena ovalifolia** Ruiz et Pav., Fl. Peruv. Chil. 1: 67. 1798. TIPO: Perú. Pillao "Huassa-huassi in humidis et umbrosis," *Ruiz et Pavón s.n.* (lectotipo, designado por Romoleroux (1996: 69), MA [Herbarium Peruvianum, Ruiz et Pavón, 10/80]!). Figura 5C, D.

Acaena elegans Gay, Hist. Chile, Bot. 2: 297. 1847. *Acaena ovalifolia* var. *elegans* (Gay) Reiche, Anales Univ. Chile 98: 169. 1897. *Acaena ovalifolia* subsp. *elegans* (Gay) Bitter, Biblioth. Bot. 17(74): 242. 1910. TIPO: Chile. "La encontramos en los cerros subandinos de la hacienda de Talcaregüe, en departamento de San Fernando (1891)," *Gay 80* (holotipo, P-106306!).

Acaena tenuipila Bitter, Biblioth. Bot. 17(74): 234. 1910. TIPO: Chile. "Prov. Valdivia, pl. chilensis, herb. Stockh., Upsal.," *Lechler 584* (lectotipo, aquí designado, S-R8072!, duplicado, CONC-29697!).

Acaena micranthera Bitter, Biblioth. Bot. 17(74): 235. 1910. TIPO: Chile. "Loco speciali non indicato, herb. Paris," *Gay s.n.* (holotipo, P, foto 34723 en CONC!).

Planta hasta 20 cm de alto; rizomas largos, ca. 2 mm de diámetro; tallos de 1.5–2.5 mm de diámetro, seríceos; entrenudos de 0.5–1 mm. Hojas de 2.3–10 cm; lámina en contorno obovada; 3–5 pares de folíolos, oblongo-elípticos a elípticos, de 7.5–32 mm de largo, base oblicua, margen aserrado, crenado, pinnatífido, con 7–10 segmentos, pilosos a seríceos en el envés, especialmente en los nervios; vainas foliares pilosas; apéndices estipulares lineares, agudos, de 3–8.5 mm de largo, el margen levemente aserrado. Rama florífera terminal; el pedúnculo hasta 10.5 cm de largo, piloso; inflorescencia capituliforme, rojiza en fruto, hasta 40 mm de diámetro; brácteas basales lineares, laciniadas, de 2.5–6 mm de largo. Flor chasmógama con sépalos 3–4, oblongos, de 1–2.5 mm de largo, cara interna serícea; estambres 2–5, filamentos de 1.2–4 mm de largo, anteras globosas, de 0.2–0.3 mm de largo; estilo de 0.5–1 mm de largo; estigma oblongoide, laciniado, de 0.5–1 mm de largo. Cupela obcónica, de 17.5–19 mm de largo, cubierta por tricomas retrorsos de color amarillo pálido, tiesos, caedizos, con 2 largas espinas de base angosta en el ápice, raro 3, de 14–15 mm de largo, con fuertes gloquidios; aquenio 1. Inflorescencia cleistógama hasta 8 mm de diámetro; flores solitarias o en grupos, pedunculadas o sésiles; sépalos de 1–1.5 mm de largo, estigma ca. 1.5 mm de largo, ovario ca. 0.5 mm de diámetro.

Icones. Grondona, 1964: fig. 4–7; 1984: fig. 449. Ruiz y Pavón, 1798: tab. 103, fig. c.

Fenología. Fructifica de agosto (*Rodríguez 843*) a marzo (*Gunckel 15348*) y en algunos casos se le puede encontrar con flores desde junio (*Gunckel 15632*).

Distribución y hábitat. Planta nativa, crece en suelo seco, a orillas de río o de camino, también en laderas húmedas, desde la IV Región (Fray Jorge) a la XII Región (Isla Navarino), de 5 a 3000 m de altitud (Fig. 11F). Se encuentra como maleza en las islas Más a Tierra y Más Afuera del Archipiélago de Juan Fernández. También crece en las Islas Falkland (Moore, 1968), en Argentina (Zardini, 1999), Ecuador (Romoleroux, 1999) y Perú (Gereau, 1993).

Nombre común. Cadillo (*Junge s.n.*; Baeza, 1921).

Caracteres distintivos. Inflorescencia capituliforme madura de color rojizo; cupela con pelos tiesos retrorsos y dos espinas apicales largas con gloquidios.

Acaena ovalifolia pertenece a la Sección *Ancistrum*. Esta especie es cercana a *A. magellanica* y *A. argentea*, con las que comparte en términos generales, el tipo de hábito, la inflorescencia y la forma de la cupela. A diferencia de ellas, *A. ovalifolia* presenta una distribución mucho más amplia en América, llegando hasta Ecuador (Romoleroux, 1999).

En relación a sus sinónimos, *Acaena tenuipila* Bitter, se examinaron especímenes de S y CONC que corresponden a *Lechler 584*, y se eligió como lectotipo a la muestra de S-R8072, porque presenta una planta con una infrutescencia madura, en tanto que la de CONC-29697 está poco desarrollada. Para las variedades *dolichacantha* Bitter, *inciserrata* Bitter y *subglabrescens* Bitter, no fue posible localizar materiales originales, y se presume que fueron destruidos ya que estaban depositados en Berlín. No obstante, al estudiar las descripciones, el autor basó sus variedades en caracteres muy variables, como la pubescencia (*subglabrescens*), el grado de división de los dientes de los folíolos (*inciserrata*) y en el largo de las espinas (*dolichacantha*). Tampoco se encontró material tipo para la variedad *serrata*, el que estaba en UPS, sin embargo sucede lo mismo que para las anteriores, fue establecida de acuerdo a caracteres

variables, en este caso los dientes agudos del folíolos. El tipo de la especie *A. subtussericacens* Bitter, estaba en B, por lo que se supone destruida. De acuerdo a la descripción la cupela presenta tres espinas, lo que a veces es posible observar en *A. ovalifolia*, además se señala que la cupela tiene pelos tiesos numerosos, un carácter propio de la especie.

Material representativo examinado. ARGENTINA. **Santa Cruz**: Glaciar Moreno, *Anliot 6141* (SGO); Güer Aike, Est. Rospentek, *T.B.P.A. 3263* (HIP). CHILE. **IV Región**: Limarí, Talinay, *Jiles 1685* (CONC). **V Región**: Valparaíso, Juan Fernández, Más a Tierra, Villagra a El Mirador, *Stuessy et al. 11777* (CONC); Más Afuera, Quebrada Sándalo, *Stuessy & Lammers 9278* (CONC); N Quebrada Casas, *Stuessy et al. 9064* (CONC); Cordón Atravesado, *Stuessy & Lammers 9214* (CONC). **VI Región**: Cachapoal, Agua de la Vida, Hda. Cauquenes, 15 Oct. 1976, *Dessauer s.n.* (SGO); Colchagua, Talcaregue, *F. Philippi s.n.* (SGO). **VII Región**: Curicó, Camino Laguna de Teno–Paso Vergara, *C. Marticorena & Matthei 961* (CONC); Talca, Altos de Vilches, *Zoellner 10379* (CONC); Linares, Valle Botacura, *Schlegel 3583* (CONC). **VIII Región**: Ñuble, Termas de Chillán, *Pfister 480* (CONC); Concepción, Chiguayante, 15 Oct. 1965, *Catalán s.n.* (CONC); Arauco, Cordillera de Nahuelbuta, Alto Los Cóndores, *Matthei & Quezada 51* (CONC); Laraquete, 1 Mar. 1936, *Junge s.n.* (CONC); Biobío, Camino de Ralco a Lepoy, *A. Marticorena et al. 299* (CONC). **IX Región**: Malleco, P. N. Nahuelbuta, *Rodríguez et al. 2083* (CONC); Termas Río Blanco, *Montero 9987* (CONC); Cautín, P. N. Los Paraguas, *A. Marticorena et al. 335* (CONC). **X Región**: Valdivia, Lago Panguipulli, Reducción Curaco, *C. Marticorena et al. 423*. (CONC); Corral, Chaihuin, *Gunckel 15632* (CONC); Misión Quinchilca, *Gunckel 15348* (CONC); Osorno, P. N. Puyehue, Refugio Antillanca, *Rodríguez 1050* (CONC); Llanquihue, P. N. Vicente Pérez Rosales, Punta Guano, *C. Marticorena et al. 1949* (CONC); Chiloé, Pulinque, *C. Marticorena 1582* (CONC); Camino entre Castro y Chonchi, km 12, *Weldt & Rodríguez 730* (CONC); Quellón, Punta Lapa, *C. Marticorena et al. 81* (CONC); Palena, Isla Talcán, *C. Marticorena 1633* (CONC). **XI Región**: Aisén, Islas Guaitecas, Melinka, *Ricardi & C. Marticorena 4096* (CONC); Camino de Pto. Chacabuco a Pto. Aisén, *Parra 1* (CONC); Coyhaique, Coihaique, *Martínez P. 18* (SGO); General Carrera, S de Laguna Fontana, *Braynshaw 221* (HIP). **XII Región**: Ultima Esperanza, Torres del Paine, Cerro Diente, *Arroyo & Squeo 860086* (CONC); Est. Dos de Enero, Valle de las Chinas, *Pisano & Cárdenas 4838* (HIP); Magallanes, Isla Riesco, Est. Río de los Palos, 4 Ene. 1921, *Pfister & Ricardi s.n.* (CONC); Península Brunswick, Laguna El Parrillar (al N), *Dollenz 991* (HIP); Isla Dawson, Puerto Harris, *Rodríguez 843* (CONC); Tierra del Fuego, Vicuña, *Ricardi & Matthei 219* (CONC); Antártica Chilena, Isla Navarino, frente islote Snipe, *Rodríguez 870* (CONC).

12. Acaena patagonica A. E. Martic., Novon 9: 227. 1999. TIPO: Chile. "Ultima Esperanza, P. N. Torres del Paine, Cerro Diente, 900 m, 15. Dic. 1985," *Arroyo & Squeo 850829* (holotipo, CONC-100000!). Figura 6C, D.

Planta hasta 20 cm de alto, con entrenudos cortos. Hojas lineares; lámina de 1.3–2.5 cm de largo; 5–8 pares de folíolos, de 3–6.5 mm de largo, obovado a obovado-orbicular, 3–5 partidos, segmentos lineares a linear-lanceolados, margen revoluto, cara superior glabrescente, con tricomas blancos esparcidos, cara inferior serícea, base cuneada; vainas foliares con el margen con tricomas separados, apéndices estipulares ausentes. Rama florífera terminal, pedúnculos hasta 16 cm de largo, pubescentes a seríceos. Inflorescencia espiciforme corta, de 6.5 mm de diámetro, con pequeños glomérulos de flores y/o frutos a lo largo del pedúnculo; brácteas basales lineares a triangulares, de 1–1.5 mm, con el márgen partido. Flor chasmógama con 4–5 sépalos, lanceolados, de 1.5 mm, cara superior glabra, cara inferior serícea, con un mechón de tricomas en el ápice; estambres 4, anteras orbiculares, de 0.3 mm; estigma orbicular, laciniado, de 0.5 mm de diámetro. Cupela ovada a casi redonda, de 1.5–2.5 mm, pubescente a glabra, 3–4 costillas, en las cuales se dispone una espina de 0.5–2 mm de largo, con tricomas retrorsos desde el ápice, dispuesta en el tercio superior de la cupela, a veces puede presentar otra espina rudimentaria bajo la principal. Aquenio 1.

Icon. Marticorena, A., 1999, fig. 1.

Fenología. Fructifica de diciembre (*Elvebakk 532*) a febrero (*Arroyo & Squeo 870189*).

Distribución y hábitat. Planta nativa, crece entre rocas, en sitios secos y también en vegas de altura en la XII Región (en la zona del Paine y en Tierra del Fuego), desde el nivel del mar hasta los 900 m de altitud (Fig. 12A). También en la Patagonia Argentina.

Caracteres distintivos. Folíolos 3–5 partidos, segmentos revolutos; cupela ovoide a redonda con 3–4 costillas poco notorias terminadas en un espina con tricomas retrorsos en el ápice.

Acaena patagonica pertenece a la Sección *Patagonica*. Especie relacionada con *A. pinnatifida*, de la que se diferencia por sus folíolos con menos segmentos y por sus cupelas con 3–4 espinas en el tercio superior. Sin embargo, el patrón celular de la cupela es distinto, y la asocia más a las especies de las Secciones *Pleurocephala*, *Subtuspapillosae* y *Acrobyssinae* (Marticorena, 2000).

Material representativo examinado. ARGENTINA. **Sta. Cruz**: Güer Aike, Est. Las Viscachas, cono Pan de Azúcar, *T.B.P.A. 2563* (HIP); Est. Cabo Buen Tiempo, *T.B.P.A. 50* (HIP). **Tierra del Fuego**: Tennessee oil camp, *Goodall 207* (LP). CHILE. **XII Región**: Ultima Esperanza, Sierra Baguales, Cerro Santa Lucía, *Arroyo & Squeo 870189* (CONC); Torres del Paine, Cerro Diente, *Arroyo & Squeo 850829* (CONC, Typus); Cerro Corona, La Victorina, Lago Paine, *Pisano 5631* (HIP); 4–5 km SE de Est. Cerro Guido, *Elvebakk 532* (CONC); Lago Sofía, *Pisano & Henríquez 6827*

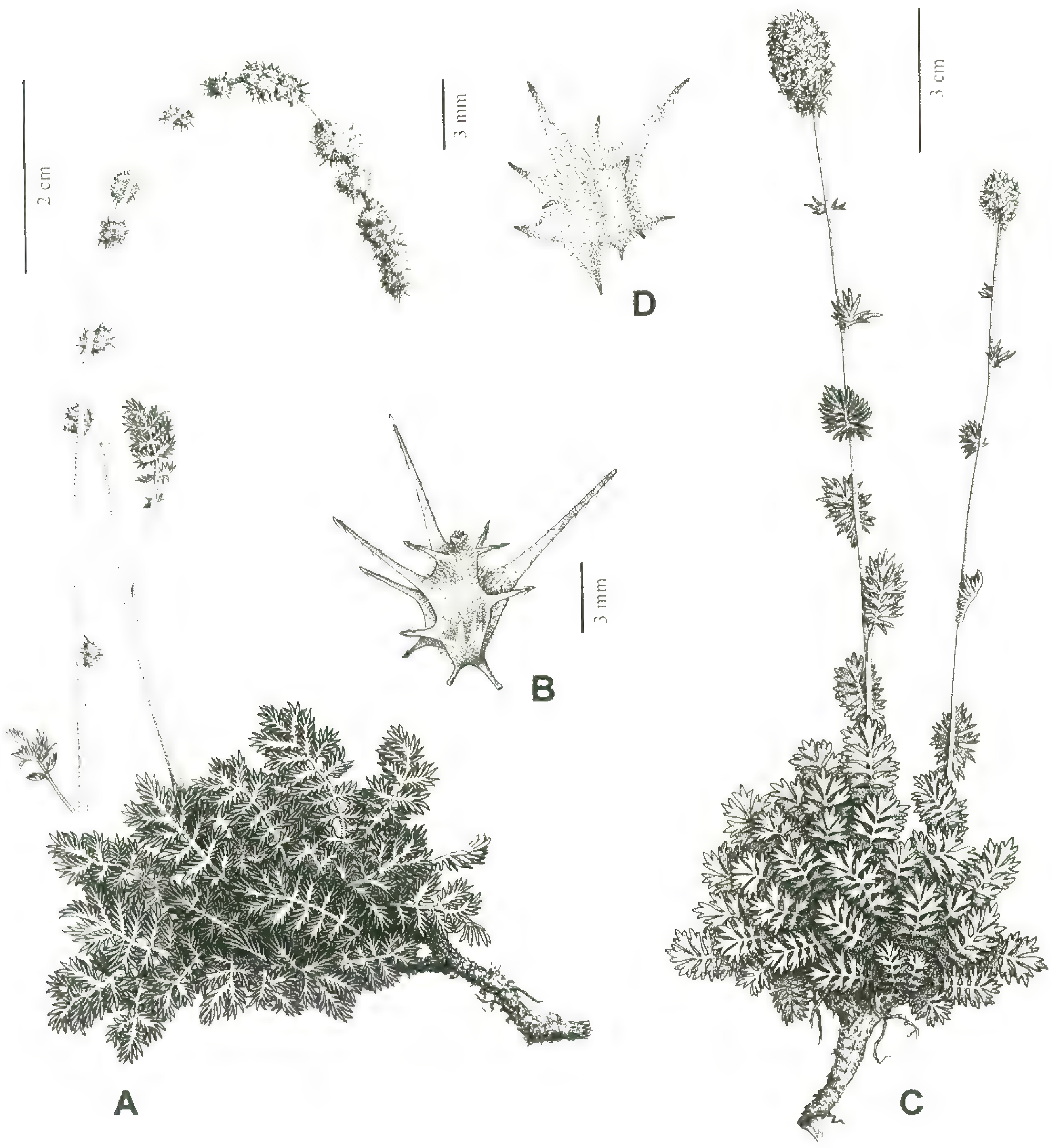

Figura 7. *Acaena pinnatifida*. —A. Hábito. —B. Cupela (*Taylor y Gereau 10907*, CONC). *Acaena trifida*. —C. Hábito. —D. Cupela (*Landrum 7932*, CONC).

(HIP); Puerto Natales, *Muñoz s.n.* (CONC); Tierra del Fuego, Punta Delgada, Buque Quemado, *Dollenz 495, 497* (HIP).

13. Acaena pinnatifida Ruiz et Pav., Fl. Peruv. Chil. 1: 68. 1798. TIPO: Chile. "Habitat in apricis et collibus Conceptionis Chile, per Puntilla, Gavilan et Hualpen tractus," *Ruiz et Pavón s.n.* (lectotipo, aquí designado, MA [Herbarium Peruvianum, Ruiz et Pavón, 10/83], foto 29605 en CONC!; duplicado, CONC-29692!). Figura 7A, B.

Acaena multifida Hook. f., Fl. Antarct. 1: 265. 1847. TIPO: Chile. "Hab. Strait of Magalhaes; Port Gregory," *Capt. King s.n.* (holotipo, K, foto 1225 en SGO!).

Acaena oligacantha Phil., Linnaea 33: 66. 1864. *Acaena pinnatifida* var. *oligacantha* (Phil.) Reiche, Anales Univ. Chile 98: 165. 1897. *Acaena pinnatifida* subsp. *oligacantha* (Phil.) Bitter, Biblioth. Bot. 17(74): 134. 1910. TIPO: Chile. "In Andibus prov. Santiago, Cord. de las Arañas, Ene. 1861," *Landbeck s.n.* (holotipo, SGO-19871!).

Acaena calcitrapa Phil., Linnaea 33: 67. 1864. *Acaena pinnatifida* var. *calcitrapa* (Phil.) Reiche, Anales Univ. Chile 98: 166. 1897. TIPO: Chile. "In Andibus de

Linares et de Talcaregue dictis crescit," colector desconocido (neotipo, aquí designado, SGO-49855!).

Acaena euacantha Phil., Anales Univ. Chile 84: 620. 1893. *Acaena pinnatifida* var. *eucantha* (Phil.) Reiche, Anales Univ. Chile 98: 165. 1897. TIPO: Chile. "In Andibus provinciae Santiago lecta est, Mar. 1883," *Philippi s.n.* (lectotipo, aquí designado, SGO-49936!; duplicado, SGO-39724!).

Acaena leptophylla Phil., Anales Univ. Chile 84: 622. 1893. *Acaena pinnatifida* var. *leptophylla* (Phil.) Reiche, Anales Univ. Chile 98: 166. 1897. TIPO: Chile. "Haud procul a thermis de Chillan dictis invenit orn., sub nom. *A. myriophylla*, Ene. 1883," *A. Borchers s.n.* (holotipo, SGO-49838!).

Acaena longifolia Phil., Anales Univ. Chile 84: 624. 1893. *Acaena pinnatifida* var. *longifolia* (Phil.) Reiche, Anales Univ. Chile 98: 166. 1897. *Acaena pinnatifida* subsp. *longifolia* (Phil.) Bitter, Biblioth. Bot. 17(74): 127. 1910. TIPO: Chile. "In Andibus provinciae Valdivia habitat, loco Queñi dicto; Ene. 1887," *Otto Philippi s.n.* (holotipo, SGO-49840!).

Acaena pinnatifida subsp. *hypoleuca* Bitter, Biblioth. Bot. 17(74): 121. 1910. TIPO: Chile. "In collibus ad San Juan, sub nom. *A. myriophylla* Lindl., herb. Berol., Brem., Paris, Stockh., Ene. 1853," *Philippi 327* (lectotipo, aquí designado, BREM!; duplicado, P!, S-R8062!).

Acaena pinnatifida var. *parvifrons* Bitter, Biblioth. Bot. 17(74): 122. 1910. TIPO: Chile. "Prope urbem Valdivia sub nom. *A. myriophylla* Lindl.-Schlecht., herb. Paris," *Lechler 294* (holotipo, P-106296!).

Acaena pinnatifida subsp. *nudiscapa* Bitter, Biblioth. Bot. 17(74): 122. 1910. TIPO: Chile. "Patagonia occidentalis: Vallis fluminis Aysén, herb. Berol., Stockh. et Upsal., 14 Ene. 1897," *P. Dusén s.n.* (lectotipo, aquí designado, S-8064!, UPS no visto).

Acaena pinnatifida var. *uspallatensis* Bitter, Biblioth. Bot. 17(74): 125. 1910. TIPO: Chile. "Uspallata-Paβ der chilenischen Hochcordillere, 33° südl. Br.: Juncal, auf den Bergen, (Baenitz, herb. Americ. nr. 1125 in herb. Brem. et Lauson. neque numerus in herb. Vratilsav.), 29 Ene. 1903," *O. Buchtien s.n.* (lectotipo, aquí designado, BREM!; duplicado, M!).

Acaena pinnatifida var. *macrura* Bitter, Biblioth. Bot. 17(74): 129. 1910. TIPO: Chile. "Prov. Colchagua, San Fernando, in collibus, herb. Paris, Dec. 1830," *Gay 81* (holotipo, P-106295!).

Acaena pinnatifida subsp. *liocarpa* Bitter, Biblioth. Bot. 17(74): 130. 1910. TIPO: Chile. "Sur les pelouses des hautes cordillères de Talcaregue, commune, terrain basaltique, fructifera, herb. Paris, Febr. 1831," *Gay 76* (holotipo, P-106294!).

Acaena pinnatifida var. *intermedia* Bitter, Biblioth. Bot. 17(74): 133. 1910. TIPO: Chile. "Hacienda Cauquenes, Cajon del Cypres, 'an den Quellen' sub nom. Acaena cfr. Poeppigiana Clos det. R. A. Philippi, herb. Monac.," *Philippi s.n.* (holotipo, M!).

Acaena pinnatifida subsp. *heterotricha* Bitter, Biblioth. Bot. 17(74): 133. 1910. TIPO: Chile. "Cordillera de Santiago, unâ cum *A. oligacantha* Phil. et *A. poeppigiana* Gay distribuit R. A. Philippi sub nomine *A. oligacantha* Phil.," *Philippi s.n.* (holotipo, W-116066!).

Acaena multifida subsp. *intercedens* Bitter, Biblioth. Bot. 17(74): 143, tab. 14b. 1910. TIPO: Chile. "Habitat freti Magellanici angustias: Punta Arenas. pl. Magell. in arenosis maritimis sub nom. '*A. pinnatifida* R. et P. – Grisebach,' herb. Paris, Ups.," *Lechler 1149* (lectotipo, aquí designado, P-106293!, duplicado, P-106300!).

Acaena multifida subsp. *quinquefida* Bitter, Biblioth. Bot. 17(74): 143. 1910. TIPO: Chile? "Regio Magellanica, Punta Arenas." *Lechler 978* (holotipo, BREM!).

Acaena multifida var. *utrinquepilosa* Bitter, Biblioth. Bot. 17(74): 144. 1910. TIPO: Chile. "Hab. in apertis caespitum, Port Famine (Détroit de Magellan, voyage de l'Astrolabe et de la Zélée, 1841), herb. Paris," *Hombron s.n.* (holotipo, P-106302!).

Planta hasta 73 cm de alto, entrenudos cortos. Hojas 4–18 cm de largo; 8–10 pares de folíolos ovado-oblongos, de 6–21.5 mm, pinnatisectos, con 5–7 pares de segmentos linear-lanceolados, revolutos en las hojas adultas, cara inferior sericea, superior pilosa, las hojas jóvenes completamente seríceas; vainas foliares vellosas en el dorso; apéndices estipulares ausentes; pecíolo notorio. Rama florífera terminal; pedúnculo del tamaño de la planta, pilosos con tricomas blancos, delgados, blandos; inflorescencia espiciforme, en general laxa, de 2.3–11 cm de largo, hasta 45 cm e interrumpida en fruto; brácteas basales lineares, de 1.5–2.5 mm de largo, pubescentes. Sépalos 4–6, oblongo-lanceolados, de 1.5–3 mm de largo, cara interna glabra, cara externa serícea, con un mechón de tricomas duros en el ápice; estambres 2–6, filamentos ca. 2.5 mm de largo, anteras globosas, de 0.5–1 mm de largo; estilo corto, estigma globoso, laciniado, ca. 1 mm de diámetro. Cupela ovoide, de 4–10 mm de largo, vellosa a tomentosa, cubierta por espinas largas, finas, de tamaño similar, sin gloquidios, con tricomas retrorsos; aquenio 1. Flores cleistógamas acompañadas por un bráctea con forma de hoja pequeña o folíolo, pinnatisecta; espinas desde reducidas a largas como en las flores chasmógamas; flores y frutos de la espiga pasan gradualmente a ser flores o frutos cleistógamos; cupelas en poca cantidad, generalmente una.

Icones. Grondona, 1964: fig. 45–49; 1984: fig. 453. Ruiz y Pavón, 1798: tab. 104, fig. c.

Fenología. Fructifica de octubre (*Garaventa 6379*) a abril (*Parra & Rodríguez 168*).

Distribución y hábitat. Especie nativa, crece en suelos arenosos, secos, entre piedras, sobre escoria volcánica, también en lugares sombríos y sitios húmedos. Habita desde la IV Región (Cordillera de Ovalle) a XII Región (Isla Navarino), desde los 5 a más de 3000 m de altitud (Fig. 12B). También en Argentina.

Nombres comunes. Cadillo (*Grandjot s.n.*), amor seco (*Pfister s.n.*), pimpinela (*Pfister 936*), pimpinela cimarrona (*Schwabe 179*; Baeza, 1921), cepacaballo (*Jiles 1585*).

Caracteres distintivos. Folíolos pinnatisectos con 5 a 7 pares de segmentos lineares; espiga larga, algo péndula.

Acaena pinnatifida pertenece a la Sección *Acaena*. Es una especie muy variable, y al igual que el tratamiento realizado por Bitter para *A. magellanica*, el autor describió numerosos taxa basados en caracteres variables.

Se estudió dos materiales tipo para *Acaena pinnatifida*, de MA y CONC, el primero fue elegido como lectotipo (foto 29605 en CONC), y comprende una planta completa bien desarrollada. Para el sinónimo *A. calcitrapa*, no se encontró material tipo, sin embargo se seleccionó la carpeta de SGO-49855 como neotipo, ya que aunque el año es 1896, posterior a su descripción (1864), corresponde con las características de la planta, además la etiqueta está determinada y escrita por Philippi como *A. calcitrapa*, y proveniente del mismo lugar. Para *A. euacantha*, se examinaron dos materiales depositados en SGO, ambas muestras estériles y con sólo una hoja, pero se eligió como lectotipo SGO-49936, debido a que es una hoja más completa. Para *A. pinnatifida* subsp. *hypoleuca*, se estudiaron los tipos de BREM, P y S. Se examinaron dos carpetas BREM, ambas de *Philippi 327*, pero una con la fecha Ene. 1853 como se señala en el protólogo, y la otra de Dic. 1854. Esta última parece ser dudosa, por lo que se descartó como material original. Se eligió como lectotipo la muestra de BREM que corresponde con la fecha, y además es una planta bien desarrollada con muchas hojas. Para *A. pinnatifida* subsp. *nudiscapa*, se eligió como lectotipo S-R8064 que corresponde a dos plantas completas y maduras. El material tipo de UPS no se vió. De la variedad *uspallatensis*, se estudió material original de M y BREM, del Buchtien, del Herbarium Americanum del Dr. Baenitz, con el número 1125, y se eligió como lectotipo la muestra de BREM, la que además de estar completa, tiene la etiqueta original de Bitter. Bajo el mismo número del Herbarium Americanum y el mismo colector, se utilizó una muestra que Bitter describió como *A. pinnatifida* subsp. *pliacantha* Bitter y su variedad *depauperata* Bitter, el que estaba depositado en WRSL, pero que no fue localizado. No obstante, por las características en la descripción original y por corresponder a la misma muestra, son reconocibles como *A. pinnatifida*. Para *A. multifida* subsp. *intercedens*, se examinaron dos materiales de *Lechler 1149* depositados en P, y se designó como lectotipo la carpeta P-106293, que tiene una planta completa con bastantes hojas.

Numerosos materiales tipo fueron depositados en Berlín, los que presumiblemente fueron destruidos durante la Segunda Guerra Mundial. Entre estos tenemos *Acaena pinnatifida* subsp. *brevispica* Bitter con las variedades *longiuscula* Bitter y *pallidiflora* Bitter, *A. pinnatifida* subsp. *hypoleuca* Bitter var. *gracilescens* Bitter, *A. pinnatifida* subsp. *mansoënsis* Bitter, *A. pinnatifida* subsp. *membranacea* Bitter y *A. pinnatifida* subsp. *mollis* Bitter var. *humilior* Bitter. Otros taxa de los cuales no se pudo localizar material tipo fueron *A. montana* Phil., material no localizado en SGO; *A. pinnatifida* subsp. *mollis* Bitter var. *elatior* Bitter en G, y *A. multifida* subsp. *abavia* Bitter según el protólogo en Z. Para *A. multifida* subsp. *multiglomerulans* Bitter, con *A. multifida* subsp. *alaticonnata* Bitter y *A. multifida* var. *ramificans* Bitter, no se localizó material tipo, el que según los protólogos se encontraba en Z, y en Z y HBG respectivamente. Grondona (1964) las reconoció como sinónimos de *A. pinnatifida*, criterio con el que se concuerda en esta revisión.

Es interesante señalar que Bitter tenía un concepto de especie muy estrecho, lo que provocó que se describiera numerosos taxa sobre la base de caracteres variables, i.e., la consistencia de las hojas (*membranacea*), el color de los sépalos y las anteras (*pallidiflora*), a lo delgado y largo del escapo (*gracilescens*), por ser suave y alta (*mollis* var. *elatior*), entre mucho otros. También se observó la presencia de inflorescencias ramificadas (CONC 143890) lo que hizo describir a Bitter (1910) la variedad *ramificans*.

Material representativo examinado. ARGENTINA. **Neuquén**: Lacar, cerro Chapelco, *Cabrera 23010, 23023* (LP); Rio Negro, Pampa del Toro, *Cabrera 20506* (CONC). **Tierra del Fuego**: Tennessee oil camp, *Goodall 140* (LP). CHILE. **IV Región**: Limarí, Cabrería, *Jiles 1585* (CONC); Cordillera de Ovalle, Río Tascadero-El Polvo, *Jiles 6370* (CONC). **V Región**: San Felipe, Jahuel, *Barrientos 1733* (CONC); Los Andes, Laguna del Inca, Portillo, *Arroyo 81271* (CONC); Valparaíso, Quintero, dunas de Ritoque, *Gunckel 22508* (CONC); Quillota, Cerro Cruz, *Garaventa 6379* (CONC). **Región Metropolitana**: Santiago, Cuesta de Chacabuco, *C. Marticorena & Weldt 612* (CONC); Cerro Abanico, Nov. 1932, *Grandjot s.n.* (CONC); Cordillera, Baños Morales, *A. Marticorena et al. 105* (CONC); Refugio Lo Valdés, *Schwabe 179* (CONC); Embalse El Yeso, *Taylor & Gereau 10907* (CONC). **VI Región**: Cachapoal, Termas de Cauquenes, 1 Nov. 1952, *Pfister s.n.* (CONC); Colchagua, Termas del Flaco, *Montero 7418* (CONC); Cardenal Caro, Pichilemu, *Saa s.n.* (CONC). **VII Región**: Curicó, Camino de El Planchón a Los Queñes, *A. Marticorena et al. 162* (CONC); Talca, Paso Pehuenches, *C. Marticorena et al. 106* (CONC); Laguna del Maule, *Parra & Rodríguez 168* (CONC); Linares, La Mina, camino al Melado, *Ricardi 2782* (CONC). **VIII Región**: Ñuble, Termas de Chillán, *Pfister 936* (CONC); Biobío, Camino de Ralco a Lepoy, *A. Marticorena et al. 296* (CONC); Nacimento, Fundo EL Tambillo, 11 Nov. 1950, *Pfister s.n.* (CONC). **IX Región**: Malleco, Entre Angol y P. N. Nahuelbuta, *Taylor et al. 10383* (CONC); Termas de Manzanares a Lonquimay, km 26, *Ricardi & C. Marticorena 5007* (CONC); Cautín, Volcán Llaima, *Montero 12117* (CONC). **X Región**: Valdivia, Huahum, Ene. 1887, *O. Philippi s.n.* (SGO); Osorno, Cordillera de Ranco, Queñi, Ene. 1887, *O. Philippi s.n.* (SGO); Palena, 43.4 km SE de Puerto Ramirez, *Stuessy et al. 7257* (CONC). **XI Región**: Coyhaique, 33.1 km E de Cisne Medio, camino La Tapera, *Stuessy et al. 7511* (CONC); Aisén, Río Exploradores, *Seki 310* (CONC); General Carrera, S of R. Ibañez, Villa Cerro

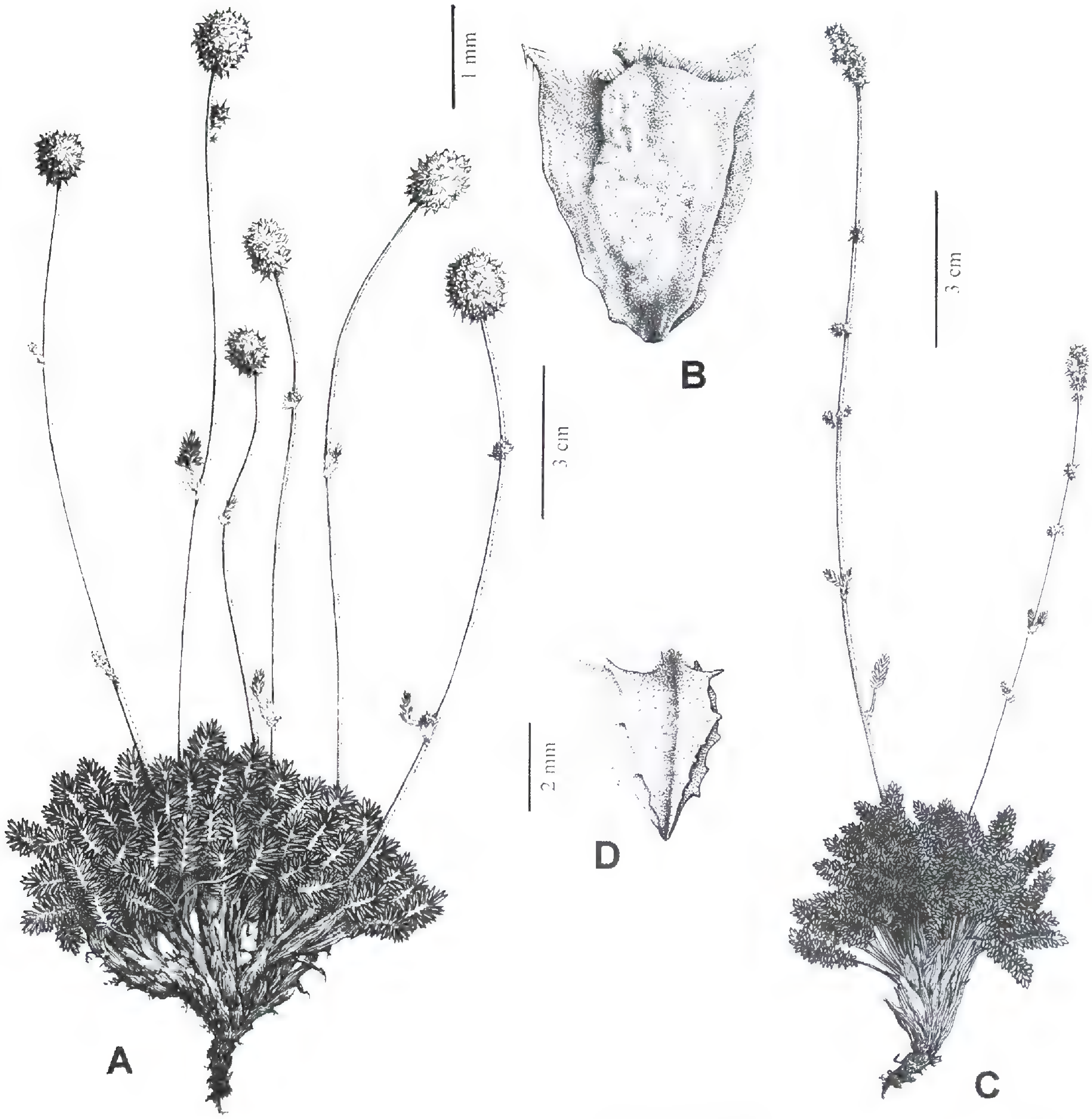

Figura 8. *Acaena platyacantha.* —A. Hábito. —B. Cupela (*Elvebakk 537*, CONC). *Acaena poeppigiana.* —C. Hábito. —D. Cupela (*Jiles 4438*, CONC).

Castillo, *Braynshaw 202* (HIP). **XII Región**: Ultima Esperanza, Cordillera de Paine, *Von Bohlen & Cavieres 337* (CONC); Sección Lazo, Cerro Toro, *Pisano 4121, 4122* (HIP); Lago Sofía, *Pisano & Henríquez 6843* (HIP); Magallanes, Punta Delgada, *Landrum 8446* (CONC); Cordonier, *Pisano 4187* (HIP); Tierra del Fuego, Río Chico, *Pisano & Henríquez 6755* (HIP); Antártica Chilena, Puerto Williams, Isla Navarino, *Tsujii 284* (CONC).

14. Acaena platyacantha Speg., Revista Fac. Agron. Univ. Nac. La Plata 3(30–31): 515. 1897. TIPO: Argentina. "Santa Cruz, Golfo de San Jorge, anno 1896. *C. Ameghino s.n.*" (lectotipo, aquí designado, LP-12682!). Figura 8A, B.

Planta erecta, hasta 20 cm de alto, raro más, tallo cubierto por las hojas; entrenudos cortos. Hojas hasta 7.2 cm de largo; lámina en contorno oblonga; 5–8 pares de folíolos, obovados, de 3–12 mm de largo, pilosos a seríceos con tricomas blancos, tripartidos, el margen revoluto; segmentos lanceolados, el central de mayor tamaño que los laterales; vainas foliares con tricomas largos y blancos en el margen, el dorso piloso; apéndices estipulares ausentes. Rama florífera terminal; pedúnculo hasta 9.2 cm de largo, raro más, seríceo, con tricomas blancos, blandos, largos, delgados; inflorescencia capituliforme, hasta 19 mm de diámetro, con flores aisladas a lo largo del pedúnculo; brácteas basales lineares a ovadas, de

2–3 mm de largo, pubescentes. Sépalos 5, oblongo-elípticos, de 1.5–2.5 mm de largo, glabros en la cara interna y pubescentes en la externa, con un mechón de tricomas blancos en el ápice; estambres 2–3, filamentos ca. 0.5 mm de largo, anteras globosas, ca. 0.5 mm de largo; estigma globoso, laciniado, ca. 0.7 mm de diámetro. Cupela ovoide-oblongoide, de 3–7.5 mm de largo, tri-tetrágona con ángulos aliformes, cubierta de tricomas cortos, duros, con 1 (raro 2) espina de base ancha en cada ángulo y dispuestas en el tercio superior de la cupela, con espinas pequeñas entre las espinas mayores y generalmente rugosa entre los ángulos con pequeñas áreas hundidas, de forma irregular y de color oscuro; aquenio 1.

Icones. Grondona, 1964: fig. 37–40; 1984: fig. 450.

Fenología. Fructifica de diciembre (*Landero 671*) a febrero (*Zoellner 7566*).

Distribución y hábitat. Crece en lugares secos desde Malleco, Paso Pino Hachado (IX Región) a Seno Skyring (XII Región), desde alrededor de 50 a 1290 m de altitud (Fig. 12C). También en Argentina.

Caracteres distintivos. Cupela tri a tetrágona, con ángulos aliformes, con zonas hundidas de forma irregular entre los ángulos.

Acaena platyacantha pertenece a la Sección *Acaena*. Spegazzini (1897) en su descripción original indica tres formas para la especie; *typica*, *elata* y *villosa*, pero no las tipifica. En el protólogo menciona dos lugares, para Río Santa Cruz, y Golfo San Jorge, depositados en LP. Estos materiales corresponden a dos clases de plantas algo diferentes, una con la cara superior de las hojas oscura y glabra, margen revoluto, cupela con alas o costillas con dos espinas superpuestas, subhorizontales, pubescencia corta, la que correspondería con la forma *elata* (LP-11942). Los otros materiales (LP-12682, 12577), podrían pertenecer a las otras dos formas, con folíolos verde claro, cara superior de las hojas pubescente, alas de la cupela elíptica a ovada, con una a dos espinas. He podido revisar materiales que presentan caracteres de ambas formas, los que hacen difícil definirlas como reconoció Spegazzini (1897), por lo tanto se consideraron como una sola especie sin formas. Como material tipo se eligió el espécimen LP-12682, ya que parece ser la forma más frecuente.

Material representativo examinado. ARGENTINA. **Santa Cruz**: Güer Aike, Est. Las Viscachas, cerro Las Viscachas, *T.B.P.A. 2397* (HIP); Colonia Carlos Pellegrini, Est. La Flora, *Von Thüngen 102* (LP); Santa Cruz, Bahía Gregorio, Río Gallegos, año 1882, *Spegazzini s.n.* (LP-11942, 12577). CHILE. **IX Región**: Malleco, Paso Pino Hachado, *A. Marticorena et al. 421* (CONC). **XI Región**: Aisén, Cerro Castillo, *Zoellner 7566* (CONC); General Carrera, Chile Chico, 12 Dic. 1954, *Pfister s.n.* (CONC). **XII Región**: Ultima Esperanza, 4–5 km SE Est. Cerro Guido, *Elvebakk 537* (CONC); Sierra de los Baguales, Est. la Cumbre, *Landero 671* (CONC); Magallanes, Seno Skyring, 8 Ene. 1952, *Pfister & Ricardi s.n.* (CONC).

15. Acaena poeppigiana Gay, Fl. Chile 2: 284. 1847. TIPO: Chile. "Forma céspedes en las cordilleras de Sotaquí (provincia de Coquimbo) a una altura de 9 a 10,000 piés," *Gay 527* (holotipo, P-106318!). Figura 8C, D.

Planta erecta, hasta 17 cm de alto; entrenudos cortos, cubiertos por la vainas foliares. Hojas hasta 7 cm de largo; lámina en contorno lanceolada; 5–6 pares de folíolos, ovados, de 3–3.5 mm de largo, el margen partido, con 3–5 segmentos oblongo-elípticos, glabrescentes a seríceos; vainas foliares con tricomas blancos y blandos en el margen; apéndices estipulares ausentes. Rama florífera terminal; pedúnculo hasta 15 cm de largo, piloso; inflorescencia espiciforme corta, hasta 3 cm de largo en fruto, a veces presentando flores a lo largo del pedúnculo; brácteas basales ovadas a lineares, de 2.5–3.5 mm de largo, pubescentes en los márgenes y el dorso, con tricomas de color amarillo pálido, blandos. Sépalos 4, oblongo-elípticos, de 0.7–1 mm de largo; cara interna glabra, externa con tricomas blancos y un mechón en el ápice; estambres 2–5; filamentos de 0.3–2.3 mm de largo, anteras globosas, de 0.3–0.5 mm de largo; estilo muy corto; estigma globoso, laciniado, de 0.3–0.5 mm de diámetro. Cupela ovoide-oblongoide, de 2–4 mm de largo, tri-tetrágona, cubierta por tricomas cortos, hirsutos, con 2–3 espinas grandes de base ancha en cada ángulo, de 0.5–1.5 mm de largo y entre los ángulos espinas pequeñas; aquenio 1.

Icones. Grondona, 1964: fig. 41–44; 1984, fig. 452.

Fenología. Fructifica de noviembre (*Jiles 2110*) a abril (*Pisano 2545*).

Distribución y hábitat. Crece al borde de vegas, orilla de lagunas, en suelo arenoso, formando champas. Habita en la IV Región (Limarí), en la VI y XII Región, desde 80 a 3500 m de altitud (Fig. 12C). También en Argentina.

Caracteres distintivos. Segmentos de los folíolos ovado-oblongos; cupela con 2 a 3 espinas en cada ángulo.

Acaena poeppigiana pertenece a la Sección *Acaena*. Es una especie algo variable que suele confundirse con *A. platyacantha* cuando esta crece en condiciones poco favorables, sin embargo los folíolos son inconfundibles, presentando segmentos ovados

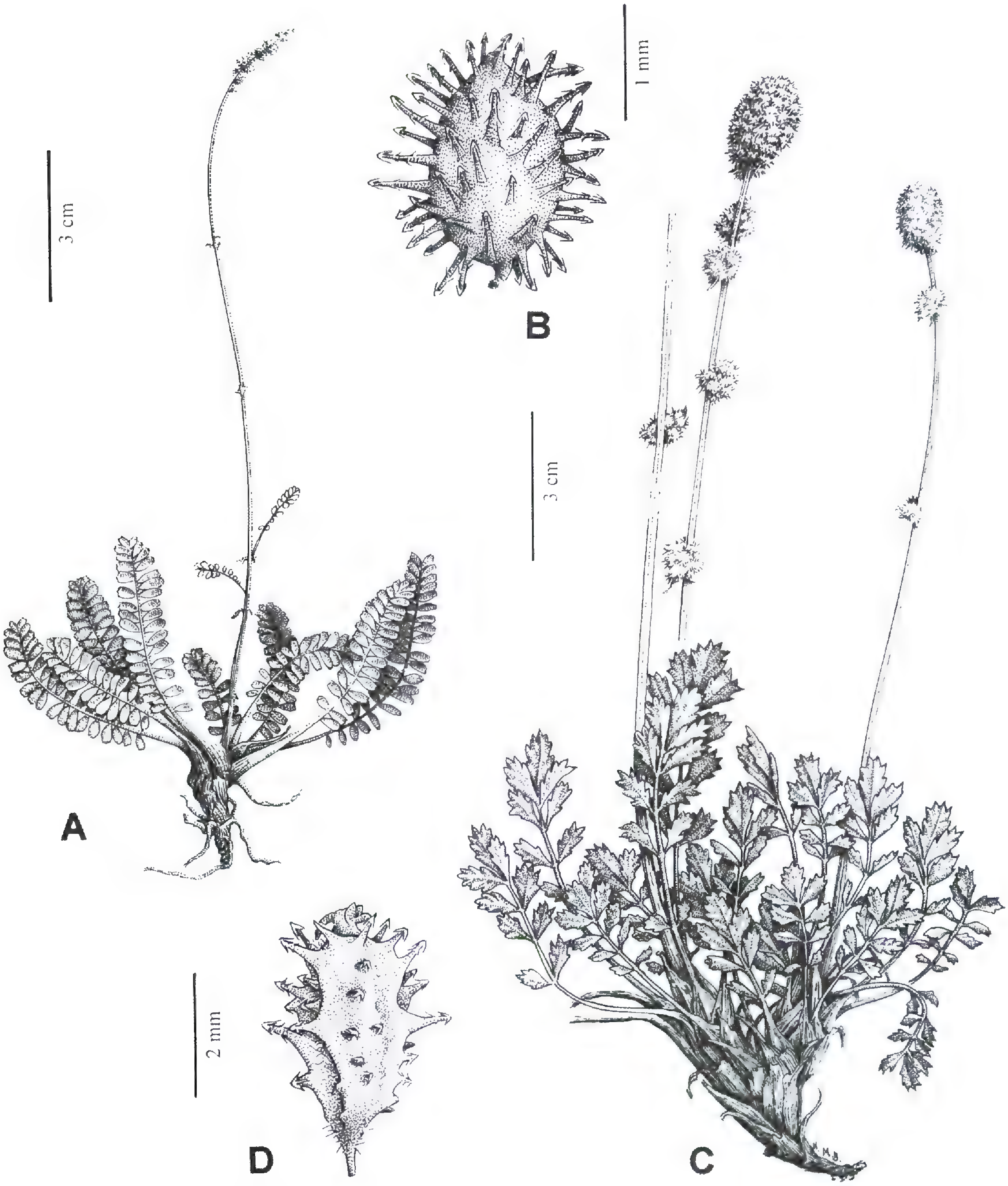

Figura 9. *Acaena pumila.* —A. Hábito. —B. Cupela (*Pisano et al. 8639*, CONC). *Acaena sericea.* —C. Hábito. —D. Cupela (*Marticorena & Matthei 599*, CONC).

característicos, además de un aspecto general más herbáceo.

Material representativo examinado. ARGENTINA. **Santa Cruz**: Colonia Carlos Pellegrini, Est. La Flora, *Von Thüngen 17* (LP). CHILE. **IV Región**: Limarí, Cordillera de Ovalle, Río Molles, *Jiles 2110* (CONC); Potrero Grande, Ramadilla, *Jiles 4438* (CONC). **VI Región**: Cachapoal, Sewell, *Pennell 12341* (SGO). **VII Región**: Linares, Cordillera de Linares, Ene. 1886, *Germain s.n.* (SGO). **XII Región**: Ultima Esperanza, P. N. Torres del Paine, Laguna Mellizas, *Elvebakk 34* (CONC); Tierra del Fuego, Est. Brazo Norte, *Pisano 2545* (CONC, HIP).

16. Acaena pumila Vahl, Enum. Pl. 1: 298. 1804. TIPO: Chile. "Habitat ad fretum Magellanicum.

Ex herbario Jussiaei, Oct.? 1767," *Commerson s.n.* (holotipo, P-106320!). Figura 9A, B.

Acaena glaberrima Phil., Linnaea 28: 685. 1858. *Acaena pumila* var. *glaberrima* (Phil.) Bitter, Biblioth. Bot. 17(74): 41. 1910. TIPO: Chile. "In insulis Chonos legit orn., 18 Ene. 1857," *Fr. Fonk 105* (holotipo, SGO-198677!).

Acaena pumila var. *acrocoma* Bitter, Biblioth. Bot. 17(74): 40. 1910. TIPO: Chile. "Adhuc solum e regione Magellanica nota: Patagonia australis: Puerto Barrow...; Peninsula Brunswick; Port Famine, herb. Lambert (herb. Upsal)," *Lambert s.n.* (holotipo, UPS!).

Planta hasta 30 cm de alto; tallo erecto, cubierto por las vainas. Hojas en contorno lineares, de 3.5–7.5 cm de largo; 9–12 pares de folíolos, orbiculados, base asimétrica, de color verde grisáceo, de 3–7.5 mm de largo, el margen revoluto, lobulados, glabros; vainas foliares glabras; apéndices estipulares ausentes. Rama florífera terminal; pedúnculo de 17.5–29 cm de largo, glabro a glabrescente; inflorescencia espiciforme, laxa, ca. 1.5 cm de largo; brácteas basales glabras, de 1.5–2 mm de largo, con 2–3 lóbulos desiguales. Sépalos 4, ovado-orbiculares, de 0.8–1.2 mm de largo, rojizos, glabros; estambres 2–4, filamentos ca. 0.2 mm de largo, anteras globosas, ca. 0.2 mm de largo; estilo ca. 0.3 mm; estigma globoso, laciniado, ca. 0.2 mm de diámetro. Cupela ovoide, de 2–2.5 mm de largo, glabra, cubierta completamente por espinas cortas de tamaño similar, con gloquidios; aquenio 1.

Icones. Grondona, 1964: fig. 50–51; 1984: fig. 454.

Fenología. Fructificación de diciembre (*Pisano 6558*) a marzo (*Henríquez & Palma 98*).

Distribución y hábitat. Crece en cojines en zonas pantanosas, vegas y turbales, desde Valdivia (Cordillera Pelada de Chaihuín) a la XII Región (Isla Hornos), de los 5 a más de 1000 m de altitud (Fig. 12D). También crece en las Islas Falkland (Moore, 1968).

Caracteres distintivos. Folíolos orbiculares, lobulados, cara inferior con células papilosas; hojas con 9–12 pares de folíolos; cupela cubierta de espinas cortas, gruesas, con gloquidios.

Acaena pumila pertenece a la Sección *Subtuspapillosae*, la que también incluye a *A. exigua* A. Gray de Hawaii, que se diferencia de la anterior por la ausencia de gloquidios en las espinas, y un menor número de folíolos. Bitter (1910) incluyó además a *A. masafuerana* dentro de la sección, pero posteriormente se estudió material fértil, que la ubicó dentro de la sección *Acrobyssinae*.

Material representativo examinado. CHILE. **X Región:** Valdivia, Mon. Nat. Alerce Costero, *Gardner & Knees 4168* (CONC); Chiloé, Pilmaiquén, *Junge 328* (CONC). **XI Región:** Capitán Prat, Caleta Tortel, parte alta en una turbera, *Rodríguez y Teneb 4077* (CONC). **XII Región:** Ultima Esperanza, Isla Wellington, Fiordo Triple, *Dollenz 1106* (HIP); Bahía Micaela, Isla Saumarez, Canal Grappler, *Pisano 6558* (CONC, HIP); Magallanes, Fiordo Nevado, Isla Santa Inés, Bahía Havergal, *Pisano & Henríquez 6633* (HIP); Tierra del Fuego, Lago Fagnano, orilla oeste, *Skottsberg 225* (SGO); Fiordo Parry, P. N. Alberto de Agostini, Caleta Alacaluf, *Pisano et al. 8639* (CONC); Antártica Chilena, Fiordo Contralmirante Martínez, brazo SE, *Henríquez & Palma 98* (CONC); Puerto Williams, Bahía Windhond, *Schlegel 8197* (CONC); Isla Navarino, Puerto Toro, *Dollenz 405* (CONC); Isla Grevy, Rada Norte, Bahía Gretton, *Pisano 5389* (HIP); Isla Hornos, Cabo de Hornos, *Dollenz 918* (HIP).

17. Acaena sericea J. Jacq., Ecl. Pl. Rar. 1: 81, tab. 55. 1816. TIPO: "*Acaena sericea*. HB 1812. Herbar. Jacquin fil." (neotipo, aquí designado, W!). Figura 9C, D.

Acaena cuneata Hook. et Arn., Bot. Misc. 3: 307. 1833. TIPO: Chile. "Cordillera of Chili, Cuming (N. 300), near Los Ojos de Agua y Cordillera (1832)," *Bridges 4* (lectotipo, aquí designado, GL, foto 3689 en SGO!; isotipo, K, foto 1228 en SGO!).

Acaena fuegina Phil., Anales Univ. Chile 84: 620. 1893. TIPO: Argentina. "In Fuegia orientali legit musei famulus," *Pablo Ortega s.n.* (lectotipo, aquí designado, SGO-49831!; duplicado, SGO-39704!).

Planta hasta 35 cm de alto; rizoma leñoso; entrenudos cortos. Hojas en contorno oblonga, de 4–10 cm de largo; 3–5 pares de folíolos de color verde oscuro, obovados, de 7–13 mm de largo, base cuneada, ápice inciso con 3–5 segmentos, pubescentes a seríceos; vainas foliares de margen piloso; apéndices estipulares ausentes. Rama florífera terminal, hasta 31 cm de largo, pilosa; pedúnculo de 12–31 cm de largo; inflorescencia capituliforme, hasta 15 mm de diámetro; brácteas basales ovado-lanceoladas, de 1.5–4 mm de largo, cara externa pubescente, cara interna glabra, con tricomas largos, amarillos. Sépalos 5–6, oblongo-elípticos, de 1.4–3 mm de largo, pubescentes como las brácteas basales, la cara interna brillante; estambres 2–5; estilo ca. 0.3 mm de largo; estigma globoso, laciniado, de 0.5–0.7 mm de diámetro. Cupela obovoide, piriforme, de 3.5–5 mm de largo, glabra a pubescente con tricomas cortos, con 4–5 costillas y 4–5 espinas duras en cada una, de base ensanchada, más largas en la parte superior de la cupela, con gloquidios; aquenio 1. Flores cleistógamas, en ramas floríferas basales dispuestas en vainas foliares en número de 1–5.

Icones. Grondona, 1964: fig. 58–60; 1984: fig. 457.

Fenología. Fructifica de noviembre (*B. Parra 476*) a enero (*Marticorena & Matthei 599*).

Distribución y hábitat. Planta nativa, habita en la

V Región (Los Andes) a la Región Metropolitana (Cajón del Maipo), y en la XII Región, desde 200 a 2600 m de altitud (Fig. 12D). Crece en suelo arenoso y en la zona sur en estepa de Mulinum (*Pisano & Cárdenas 4818*), entre pastos duros y arbustos, como rosetas aisladas. También en Argentina.

Caracteres distintivos. Cupela obovoide, con 4–5 costillas y 4–5 espinas en cada una, cortas, de base ensanchada.

Acaena sericea pertenece a la Sección *Acaena*. Jacquin (1816) describe la especie desde material cultivado en el Jardín Botánico de París, y señala que no conoce su origen, pero la consideró distinta de las demás. La descripción viene acompañada de una lámina que se reconoce como la especie. De Candolle (1825) la cita para "Nova-Hispania, ad portum Desideratum," la que se pensó era una localidad mexicana. Bitter (1910) señala que la especie debió ser de Patagonia, Puerto Deseado, Argentina. Debido a que sólo se contaba con una lámina, en la búsqueda de material para neotipificar se localizó una carpeta del herbario de Viena que presenta una muestra completa de la planta, donde la etiqueta señala *A. sericea*, con la fecha 1812 anterior a la descripción (1816), y el nombre impreso Herbar. Jacquin fil., por lo que se consideró que cumplía con las características del protólogo.

Dentro de los sinónimos, para *Acaena cuneata* se pudo examinar dos fotos de material tipo depositados en K y GL, donde ambos ejemplares se encuentran en buen estado, pero se eligió el material de K por tener más información original incluida en la carpeta. Para *A. fuegina* pude ver dos materiales tipo de *Ortega*, ambos depositados en SGO, de los cuales se eligió como lectotipo al SGO-49831 por presentar dos plantas completas y etiquetas originales.

Philippi (1893) describió *Acaena sericea* Phil., pero ya existía la especie de Jacquin (1816). Dusén (1900) le da el nombre nuevo *A. philippi* Dusén. Según Bitter, dicha especie es sinónimo de *A. sericea* J. Jacq.

Material representativo examinado. ARGENTINA. **Mendoza**: Puente del Inca, *Ruiz Leal & Dawson 122* (LP); Trayecto desde Las Loicas hasta Paso Pehuenches, *Villagrán et al. 8176* (CONC). **Santa Cruz**: Güer Aike, Est. Las Viscachas, *T.B.P.A. 2445* (HIP). **Tierra del Fuego**: Cabo Domingo, N side, *Moore 2499* (HIP); Tennessee oil co., *Goodall 506* (LP). CHILE. **V Región**: Los Andes, 4 km antes de Portillo, *C. Marticorena & Matthei 599* (CONC); Valparaíso, Recreo Alto, *B. Parra 476* (CONC). **Región Metropolitana**: Cordillera, Cajón del Maipo, 1 km abajo de Embalse del Yeso, *Landrum & Martínez 8227* (SGO). **XII Región**: Ultima Esperanza, Sierra Baguales, Est. Dos de Enero, *Pisano & Cárdenas 4818* (HIP); Sierra Baguales, Cerro Santa Lucía, *Arroyo et al. 841072* (CONC, HIP); Magallanes, Escorial de Pali Aike, Cerro Diablo, *Pisano 5185, 5222* (HIP); Río Pescado, Islote Sin Nombre, *Pisano 2787* (HIP); Tierra del Fuego, Punta Espora, *Pisano & Dollenz 4515* (HIP).

18. Acaena splendens Hook. et Arn., Bot. Misc. 3: 306. 1833. TIPO: "Cordillera of Chili. Herb. Cuming (N.299); who finds it also at Sierra Bella Vista, Aconcagua (1832)," *Bridges 3* (lectotipo, aquí designado, K!; duplicado, GL, foto 3686 en SGO!). Figura 10A, B.

Acaena splendens var. *gracilis* Bitter, Biblioth. Bot. 17(74): 81. 1910. TIPO: Chile. "Cordill. de los Andes, sub nom. '*A. argentea*?' herb. Vindob.," *Bridges 3* (holotipo, W!).

Acaena splendens var. *brachyphylla* Bitter, Biblioth. Bot. 17(74): 81. 1910. TIPO: Chile. "Prov. Aconcagua, inter fragmenta syenitica ad nives perpetuas, Estero del Peñon rasgado, Cordill. de Sa. Rosa unâ cum *A. digitata* Phil. ambae sub nom. '*A. alpina*' Poepp. pl. chil. exs. diar. 517," *Poeppig 131* (lectotipo, aquí designado, W-359497!; duplicado, W-359498!).

Acaena splendens var. *macrophylla* Bitter, Biblioth. Bot. 17(74): 82. 1910. TIPO: Chile. "Cordill. de Santiago, herb. Vindob.," *Philippi s.n.* (holotipo, W-116061!).

Acaena splendens var. *brevisericea* Bitter, Biblioth. Bot. 17(74): 82. 1910. TIPO: Chile. "Cordill. de Maule, herb. Delessert in herb. Genev., Vindob. (1855)," *Ph. Germain s.n.* (lectotipo, aquí designado, W-110770!).

Planta hasta 44 cm de alto; entrenudos cortos. Hojas de 6.7–13 cm de largo, de aspecto palmado; 2–4 pares de folíolos, 1° y 2° par de folíolos separados por más de 2 mm, lanceolados, raquis notorio, de 8–26 mm de largo, seríceos, de color verde claro, el margen entero en la parte inferior del folíolo, parte apical entera o con 3–22 dientes; vainas foliares seríceas; apéndices estipulares ausentes. Rama florífera terminal; pedúnculo hasta 43 cm de largo, seríceo; inflorescencia espiciforme, laxa; brácteas basales lineares, seríceas, de 3.5–4.5 mm de largo. Sépalos 5, lanceolados, de 2.5–4 mm de largo, seríceos en la cara externa, glabros en la interna; estambres 3–6, filamentos 3–4 mm de largo, anteras ovoides, de 0.5–0.7 mm de largo; estilos generalmente 2, uno con cada ovario, estigma globoso, laciniado, de 0.5–1 mm de diámetro. Cupela oblongoide-elipsoide, de 4.5–12 mm de largo, café claro, con tricomas largos, lanosos, brillantes, cubierta por espinas de tamaño similar, de 1–2.5 mm de largo, de color café rojizo, con gloquidios y tricomas retrorsos; aquenios 2. Presencia de flores cleistógamas protegidas por vainas foliares; cupelas cleistógamas del mismo tamaño y aspecto de las chasmógamas.

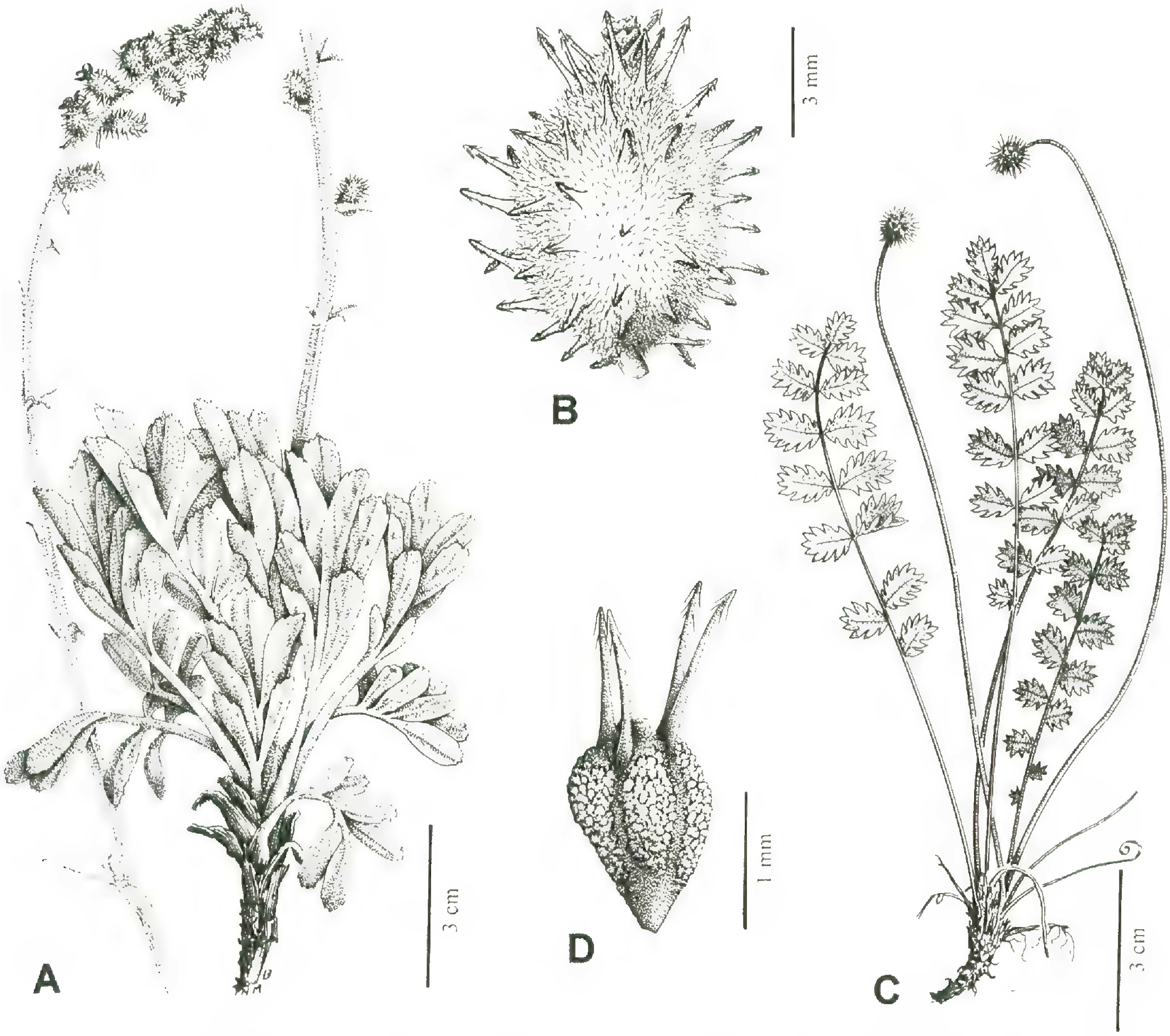

Figura 10. *Acaena splendens*. —A. Hábito. —B. Cupela (*Taylor y Gereau 10948*, CONC). *Acaena tenera*. —C. Hábito. —D. Cupela (*Schlegel 8134*, CONC).

Icones. Grondona, 1964: fig. 61; 1984: fig. 456.

Fenología. Fructifica de diciembre (*Baeza 279*) a febrero (*Ricardi 3249*).

Distribución y hábitat. Planta nativa, crece en lugares húmedos, desde la IV Región (Loica) a la VII Región (Los Queñes) desde 800 a 2400 m de altitud (Fig. 12E). También en Argentina.

Nombres comunes. Abrojo, cadillo, chonchi (*Behn s.n.*), amores secos, cepacaballo (Baeza, 1921).

Caracteres distintivos. Hojas seríceas, de color verde claro; folíolos enteros o con hasta 22 dientes pequeños en la mitad superior; cupela oblongoide, cubierta de espinas.

Acaena splendens pertenece a la Sección *Acaena*. Esta especie es similar a *A. alpina*, y suelen confundirse debido a la similitud de sus hojas, tanto en la forma de los folíolos como en su pubescencia. Sin embargo, se diferencia por la forma de la hoja que es pinnada y las cupelas ovadas, con espinas de color marrón claro.

Se pudo examinar dos materiales originales de *Acaena splendens*, depositados en K y GL. Se eligió como lectotipo el de K, que comprende tres plantas bien desarrolladas, y además los datos de colección están escritos directamente sobre la carpeta.

Para el sinónimo *Acaena splendens* var. *brachyphylla*, he visto dos materiales de *Poeppig 131*, depositados en W, de los cuales se eligió como lectotipo la carpeta W-359497, que presenta dos plantas con la espiga desarrollada. Respecto de la variedad *breviserícea*, en el protólogo se mencionan materiales originales depositados en W y G, y se designó como lectotipo la carpeta W-110770 que tiene dos plantas completas, con las espigas con flores maduras. Dentro de los sinónimos, no se pudo localizar material tipo para las variedades *angustior*

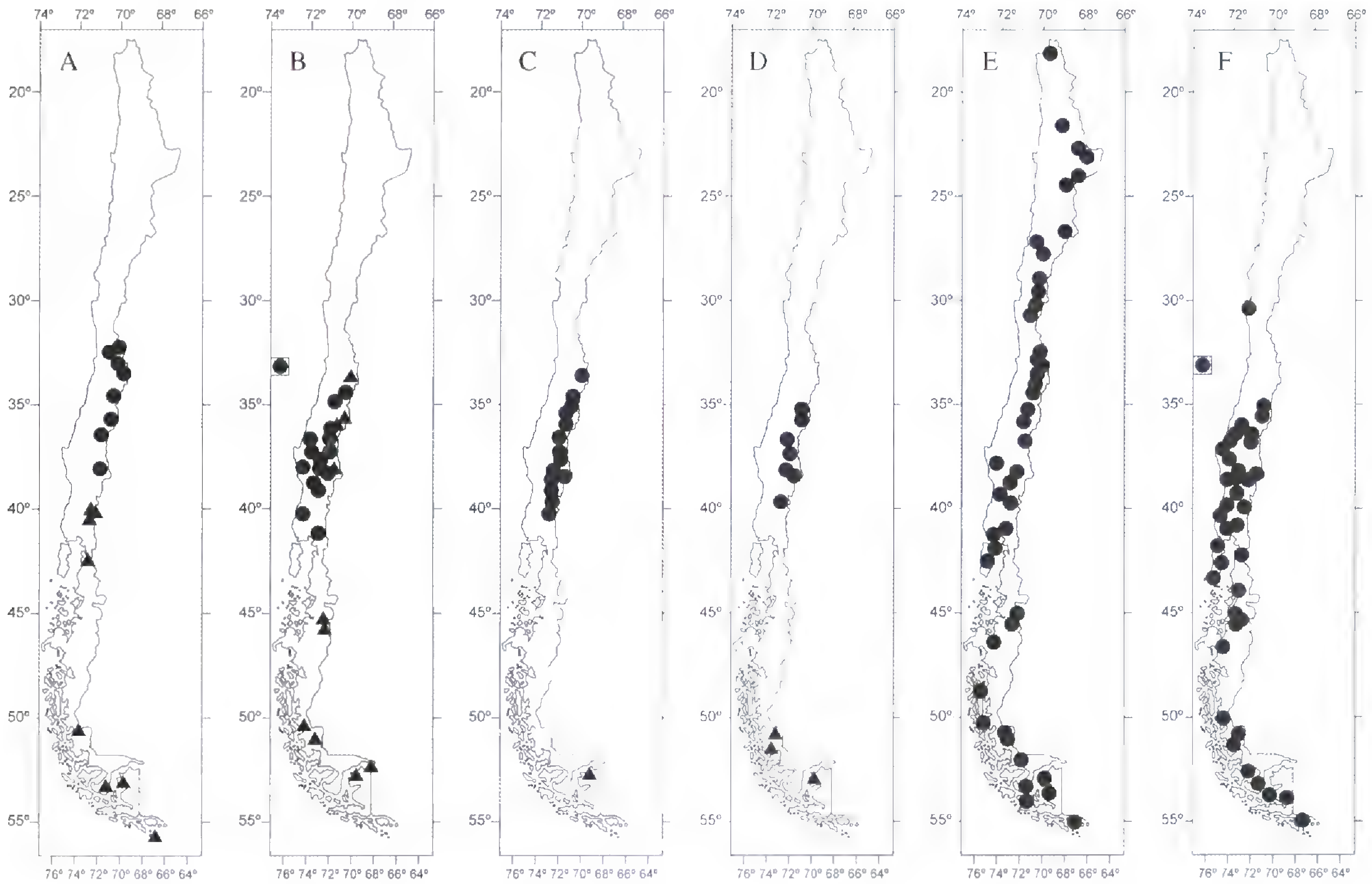

Figura 11. Mapas de distribución para las especies de *Acaena* presentes en Chile. —A. *Acaena alpina* (●); *A. antarctica* (▲). —B. *Acaena argentea* (●); *A. integerrima* (▲). —C. *Acaena caespitosa* (▲); *A. leptacantha* (●). —D. *Acaena lucida* (▲); *A. macrocephala* (●). —E. *Acaena magellanica*. —F. *Acaena ovalifolia*.

Bitter y *subintegra* Bitter, las que según los protólogos estaban depositadas en HBG y P, respectivamente. Ambas fueron descritas sobre la base de caracteres variables de la especie, tales como el margen casi entero de los folíolos (*subintegra*) o por lo angosto de ellos (*angustior*).

Material representativo examinado. CHILE. **IV Región**: Limarí, Loica, *Jiles 4725* (CONC). **V Región**: San Felipe, Jahuel, *Barrientos 1761* (CONC); Los Andes, Portillo, El Juncal, *Simon 199* (SGO). **Región Metropolitana**: Santiago, Quebrada de San Ramón, 1 Nov. 1879, *F. Philippi s.n.* (SGO); Cordillera, Lagunillas, *Beckett et al. 4471* (SGO); Cordillera, along Embalse El Yeso, *Taylor & Gereau 1948* (CONC); Subida a Potrero Grande, 8 Dic. 1933, *Behn s.n.* (CONC). **VI Región**: Cachapoal, El Pangal, *Zoellner 10142* (CONC); Colchagua, Termas del Flaco, *Baeza 279* (CONC); San Fernando, Vegas del Flaco, *Ricardi 3249* (CONC). **VII Región**: Curicó, Camino de Los Queñes a El Planchón, *A. Marticorena et al. 135* (CONC).

19. Acaena tenera Alboff, Revista Mus. La Plata 7: 367. 1896. TIPO: Argentina. "In regione alpina montis Pyramidis (supra torrentum Ushuaïa), 29 Feb. 1896," *Alboff 234* (lectotipo, aquí designado, LP-28054!). Figura 10C, D.

Acaena antarctica var. *laxiuscula* Bitter, Biblioth. Bot. 17(74): 54, tab. 3a. 1910. TIPO: Chile. "Fuegia: in alpinis prope Rio Azopardo, unâ cum *A. tenerâ* Alb. subsp. *epilis* Bitt., exped. suec. 1907/09, 3.3. 1908," *Skottsberg 208* (holotipo, SGO-58850!).

Planta hasta 15 cm de alto, entrenudos cortos. Hojas en contorno lineares, hasta 10 cm de largo; 5–8 pares de folíolos, ovados, de 5–8 mm de largo, hacia la base subopuestos, pinnatipartidos a pinnatisectos, con 7–12 segmentos lobados, de 1.5–2 mm de largo, base asimétrica, con un mechón de tricomas pluricelulares, glandulares; vainas foliares glabras; apéndices estipulares lobados, de 1.5–2 mm de largo. Rama florífera terminal; pedúnculo hasta 14 cm de largo, glabro; inflorescencia capituliforme, de 5.5–6.5 mm de diámetro; brácteas basales orbiculares, lineares o lanceoladas, con el ápice dentado, de 0.5–2 mm de largo. Sépalos 3, ovados, de 1–1.5 mm de largo; estambres y anteras no vistos; estigma globoso. Cupela obovoide, tetrágona, de 1–1.5 mm de largo, sin las espinas, hasta 3 mm de largo con las espinas, con la superficie cubierta de glándulas sésiles esféricas de color naranjo (manná), 4 espinas de base angosta en el ápice, ca. 1 mm de largo, con fuertes gloquidios; aquenio 1.

Icones. Grondona, 1984: fig. 455. Skottsberg, 1905: tab. 1–2.

Fenología. Fructifica de diciembre (*Pfister & Ricardi s.n.*) a febrero (*Pisano et al. 8271-A*).

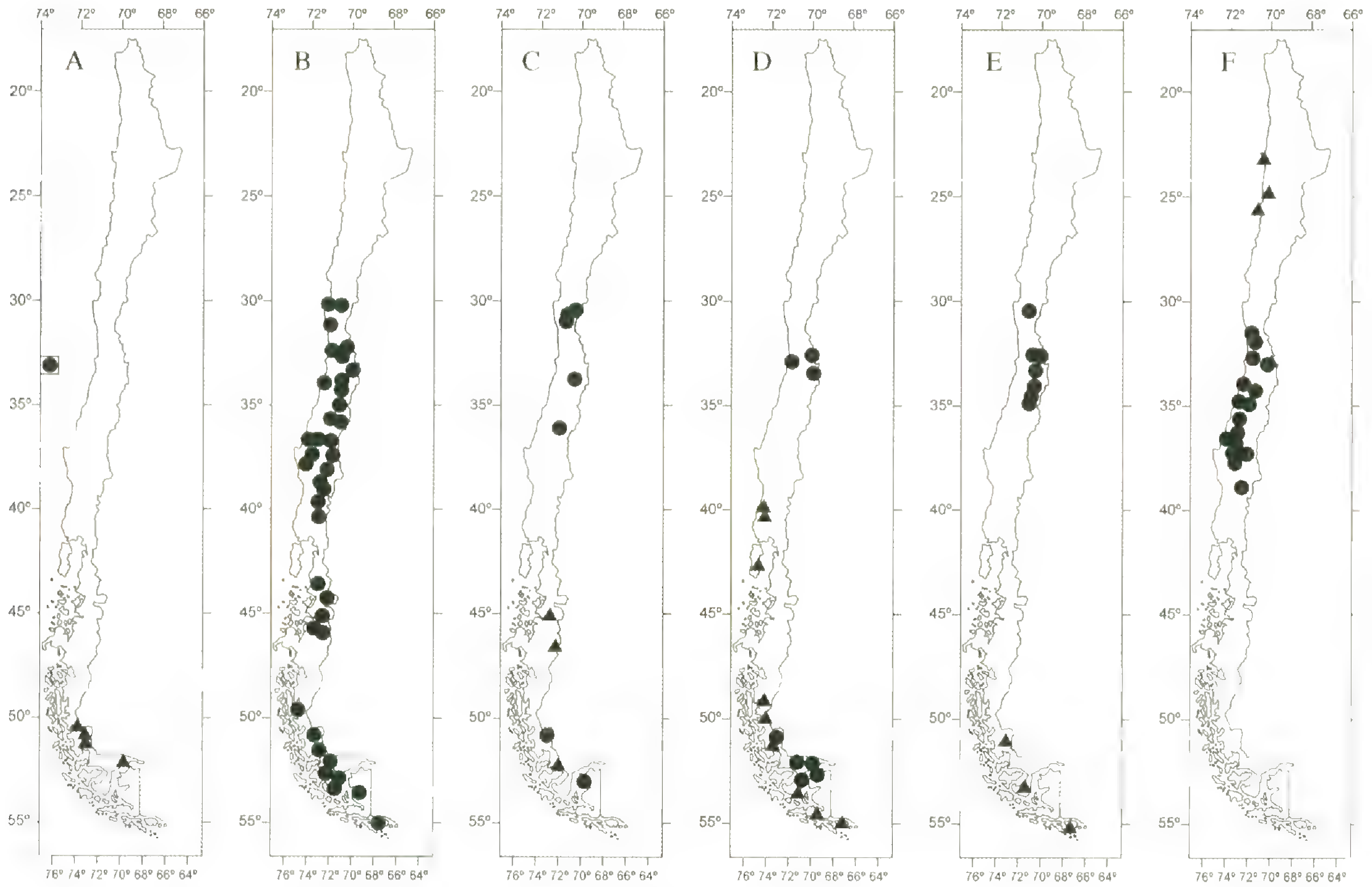

Figura 12. Mapas de distribución para las especies de *Acaena* presentes en Chile. —A. *Acaena masafuerana* (●); *A. patagonica* (▲). —B. *Acaena pinnatifida* (●). —C. *Acaena platyacantha* (▲); *A. poeppigiana* (●). —D. *Acaena pumila* (▲); *A. sericea* (●). —E. *Acaena splendens* (●); *A. tenera* (▲). —F. *Acaena trifida* (●); *A. trifida* var. *glabrescens* (▲).

Distribución y hábitat. Planta nativa, habita en la XII Región, desde 120 a 700 m sobre el mar, en sitios húmedos y entre cojines *Bolax gumifera* (Fig. 12E). También crece en Argentina y en las Islas South Georgia (Greene, 1964).

Caracteres distintivos. Cupela con glándulas esféricas (manná); folíolos con un mechón de tricomas pluricelulares en la base, la que es asimétrica.

Acaena tenera pertenece a la Sección *Acrobyssinae*. Especie poco recolectada, parecida a *A. antarctica* y a *A. masafuerana*, de las cuales se diferencia fácilmente por un mechón de tricomas glandulares en la axila de los folíolos y por las glándulas esféricas (manná) en la superficie de la cupela. Según Walton (1979), esta especie hibridiza con *A. magellanica*. Respecto del sinónimo *A. antarctica* var. *laxiuscula*, Walton (1975) la consideró sinónimo de *A. antarctica*, sin embargo las características de las hojas y cupela son claramente de *A. tenera*.

Para la subespecie *pilosella* Bitter, no fue señalado el herbario donde fue depositado, y no fue posible localizar el tipo. No obstante, Bitter (1910) describió la subespecie basado en la pilosidad de los folíolos, carácter muy variable. El autor incluyó una foto que claramente concuerda con la especie.

Material representativo examinado. ARGENTINA. **Tierra de Fuego**: S side of Lago Fagnano, Monte Heuhuepen, *Moore 2828* (HIP). CHILE. **XII Región**: Ultima Esperanza, Sierra del Toro, *Arroyo et al. 92-146* (CONC); Magallanes, Punta Arenas, 31 Dic. 1951, *Pfister & Ricardi s.n.* (CONC); Tierra del Fuego, Sector Río Cóndor, *Pisano et al. 8271-A* (CONC); Antártica Chilena, Isla Navarino, Puerto Williams, Cerro Bandera, *Schlegel 8134* (CONC).

20. Acaena trifida Ruiz et Pav., Fl. Peruv. Chil. 1: 67. 1798. TIPO: Chile. "Habitat in Regni Chilensis pascuis, campis et collibus Rere, Itatae et Conceptionis Provinciarum, ad Huilquilemu, Culenco, Penco, Talcahuano, Hualpen et Carcamo tractus," *Ruiz & Pavón s.n.* (holotipo, MA [Herbarium Peruvianum, Ruiz et Pavón, 10/82]!). Figura 7C, D.

Planta hasta 36 cm de alto; tallo cubierto por las hojas; entrenudos cortos. Hojas de 2–6 cm de largo; 4–8 pares de folíolos, ovados a obovados, de 6–13.5 mm de largo, pinnatisectos o partida, con 3–5 segmentos lineares, agudos, apéndices estipulares ausentes. Rama florífera axilar, pedúnculo piloso a pubescente, con tricomas largos, blancos, blandos; inflorescencia capituliforme; brácteas basales lineares o lanceoladas, de 2–3.5 mm de largo, con hojas pequeñas a lo largo del pedúnculo protegiendo algunas flores o frutos. Sépalos 4–6, ovado-oblongos a oblongo-lanceolados, estambres 4–6, anteras globosas, estilo corto, estigma globoso, laciniado, ca. 1 mm

de diámetro. Cupela ovoide, generalmente con 4–5 costillas con 2 espinas en cada una, base ensanchada, con tricomas retrorsos, sin gloquidios; aquenio 1.

Acaena trifida pertenece a la Sección *Acaena*. Esta especie tiene dos variedades, la var. *trifida* y la variedad *glabrescens* Regel et Körn., las cuales se diferencian principalmente por la pilosidad de los tallos y de la cupela.

Clave para las Variedades

1a. Plantas pubescentes, cupelas seríceas . . . . **A. trifida** var. **trifida**
1b. Plantas glabras, cupelas glabras . . . . **A. trifida** var. **glabrescens**

20a. **Acaena trifida** Ruiz et Pav. var. **trifida**

Acaena quinquefida Phil., Linnaea 28: 686. 1858, *Acaena trifida* var. *quinquefida* (Phil.) Reiche, Anales Univ. Chile 98: 167. 1897. TIPO: Chile. "Provincia de Valparaiso, Cordilleras de Santiago, Nov. 1854," *Germain s.n.* (lectotipo, aquí designado, SGO-49930!).
Acaena trifida var. *argentella* Bitter, Biblioth. Bot. 17(74): 102. 1910. TIPO: Chile. "Concepción, herb. Berol., Monac., Sep. 1894," *F. W. Neger 4466* (lectotipo, aquí designado, M!).
Acaena trifida var. *mollissima* Bitter, Biblioth. Bot. 17(74): 102. 1910. TIPO: Chile: "sine loco speciali indic., sub nom. *Acaena eptandrum* [sic], herb. Dombey mus. Berol., Paris," *Dombey s.n.* (lectotipo, aquí designado, P-106322!).
Acaena trifida var. *plurifoliolata* Bitter, Biblioth. Bot. 17(74): 102. 1910. TIPO: Chile: "Prov. Nuble, San Carlos, unâ cum *A. trifida* var. *nanodes* Bitt., herb. Monac.," *F. W. Neger 5099* (holotipo, M!, las dos plantas inferiores).
Acaena trifida var. *nanodes* Bitter, Biblioth. Bot. 17(74): 103. 1910. TIPO: Chile. "Prov. Nuble, San Carlos, unâ cum varietate altera: var. *plurifoliolata* Bitt. herb. Monac.," *F. W. Neger 5099* (holotipo, M!, las cuatro plantas superiores).
Acaena trifida var. *brachyphylla* Bitter, Biblioth. Bot. 17(74): 103. 1910. TIPO: Chile. "Chile australis: San Cristobal (Eisenbahnstation), herb. Monac., Stockh., (1894–95)," *P. Dusén 5100* (lectotipo, aquí designado, M!; duplicado, S, no visto).
Acaena trifida var. *robusta* Bitter, Biblioth. Bot. 17(74): 104. 1910. TIPO: Chile. "Valparaiso: Sandfläche bei Viña del Mar, pl. Chilensis in Baenitz Herb. Amer. sub nom. *A. trifida*, von Frl. Dr. Duse später als *A. pinnatifida* R. et P. bezeichnet," *Buchtien 4456* (holotipo, M!).

Hojas de 2–6 cm de largo; lámina en contorno linear-lanceolada; 7–8 pares de folíolos, ovados pinnatisectos, seríceos; vainas foliares seríceas en el dorso, cara interna glabra. Rama florífera hasta 29 cm de largo; inflorescencia de 11–14 mm de diámetro; brácteas basales de margen irregular, seríceas en la cara externa, glabras en la interna. Sépalos de 2.5–3.5 mm de largo, café rojizos, pubescentes como las brácteas basales, persistentes en el fruto; anteras de 1 mm de diámetro. Cupela de 3–6 mm de largo, serícea, con tricomas cortos, blancos.

Icon. Ruiz y Pavón, 1798: tab. 104, fig. c.

Fenología. Fructifica de septiembre (*Montero 12649*) a febrero (*Ledezma 626*).

Distribución y hábitat. Especie endémica, crece en suelo arenoso, laderas rocosas, en bosques esclerófilos abiertos, desde la provincia de Choapa (IV Región) al Volcán Villarrica (IX Región), desde aproximadamente los 15 a los 1800 m de altitud (Fig. 12F).

Nombres comunes. Pimpinela (*Pfister 277*; Baeza, 1921), amores secos (*Behn s.n.*).

En el protólogo de *Acaena quinquefida*, dice que crece en Valparaíso y Cordillera de Santiago, lo que está basado en dos carpetas depositadas en SGO. Para tipificar, se eligió la carpeta de Valparaíso por ser más representativa de su distribución y ser reconocible como la *A. trifida*.

En el protólogo de *A. trifida* var. *argentella*, se menciona materiales originales en B y M. Se presume que el material de B fue destruido, por lo tanto se eligió lectotipo la carpeta M (*Neger 4466*). Para la variedad *mollissima*, el autor menciona dos materiales, uno de Chile con duplicados en B y P, y otra muestra de Perú depositada en B. Lo materiales de B no se localizaron, presumiblemente destruidos, luego se eligió como lectotipo la carpeta de P-106322. De la variedad *brachyphylla*, se mencionan en el protólogo los herbarios M y S, de los que sólo se examinó el de M, el que fue eligido como lectotipo. El tipo de la variedad *valdiviensis* Bitter estaba depositado en B, y se supone que fue destruido.

Como ha sucedido con muchos de los taxa infraespecíficos descritos por Bitter, estos fueron basados en caracteres variables, i.e., la pilosidad de las hojas (*argentella*), por la suavidad y flexibilidad (*mollissima*), por las hojas cortas (*brachyphylla*).

Lindley (1829) describió *Acaena pinnatifida* Lindl., pero no señaló material tipo, además era un homónimo posterior por existir la especie de Ruiz y Pavón. La lámina que acompaña al texto muestra que corresponde con las características de *A. trifida*.

Material representativo examinado. CHILE. **IV Región**: Choapa, Pichidangui, *Montero 10803* (CONC). **V Región**: Petorca, Catapilco, Sep. 1865, *Philippi s.n.* (SGO); Valparaíso, 3 km N Laguna Verde, camino Valparaíso, *Lammers et al. 7761* (CONC); Lago Peñuelas, 25 Ago. 1929, *Behn s.n.* (CONC). **VI Región**: Cardenal Caro, Pichilemu, *Montero 12649* (CONC); Colchagua, La Rufina, *Montero 12648* (CONC). **VII Región**: Talca, Constitución, Dic. 1891, *Reiche s.n.* (SGO). **VIII Región**: Ñuble, 2 km al N de Quirihue, *Rodríguez 558* (CONC); Cordillera Polcura, *Ledezma 626* (CONC); Concepción, Camino de Florida a Penco, 2 km NW de Florida, *Landrum 7932* (CONC); Cerro Caracol, *Pfister 277*

(CONC); Biobío, Cordillera de Polcura, *Ledezma 626* (CONC). **IX Región**: Malleco, Angol, cerros, *Montero 5277* (CONC); Cautín, Volcán Villarrica, Ene. 1935, *Pfister s.n.* (CONC).

20b. Acaena trifida Ruiz et Pav. var. **glabrescens** Regel et Körn., Index Sem. Hort. Petrop. 1857: 8. 1858. TIPO: "Chili, *Philippi [s.n.]*" (neotipo, aquí designado, LE!).

Hojas de 2–3.4 cm de largo; lámina en contorno algo obovado; 4–6 pares de folíolos, obovados, subopuestos, de 8–12 mm de largo, 3 (4–5) partida, cara superior glabra, cara inferior glabra a algo pubescente; base ancha o de aspecto angosto por el margen revoluto, vainas foliares glabras. Rama florífera hasta 18 cm de largo, inflorescencia de 8–10 mm de diámetro; brácteas basales glabras. Sépalos de 1–1.5 mm de largo, glabros; anteras de 0.5 mm de diámetro. Cupela de (1.5)2.5–3.5 mm de largo, glabra a algo pilosa, espinas de ca. 2 mm de largo.

Fenología. Fructifica de noviembre (*Schlegel 7926*) a diciembre (*Gunckel 21873*).

Distribución y hábitat. Variedad endémica, se le encuentra desde la provincia de Antofagasta, Cerro Moreno, sector de El Rincón, Paposo, también en Chañaral, Aguada Grande y en la zona de Las Condes en la Región Metropolitana, desde los 200 a 1800 m de altitud (Fig. 12F). Es una planta escasa que crece en laderas escarpadas, en arena y entre rocas, en lugares húmedos entre fisuras.

Esta variedad fue descrita desde una planta proveniente de Chile que crecía en el Jardín Petropolitano, pero Regel y Körnicke (1858) no indicaron el tipo. El carpeta designada como tipo se encuentra depositada en LE, cuya etiqueta dice "Ex Horto bot. Petropolitano," por lo cual es muy probable que corresponda la material original. Bitter (1910) observó en el herbario de Firenze (FI) un material proveniente de Santiago y menciona que la planta en general es glabra, pero presenta algunos pelos con el ápice esférico, compuestos por muchas células.

Material representativo examinado. CHILE. **II Región**: Antofagasta, Cerro Moreno, *Zoellner 5016* (CONC); Cerro El Rincón, *Quezada & Ruiz 153* (CONC); Quebrada Peralito, *Quezada & Ruiz 373* (CONC); Paposo, Quebrada Guanillos, *Schlegel 7926* (CONC); Quebrada Agua Grande, entre Pan de Azúcar y Caleta Esmeralda, *Pisano & Bravo 586* (CONC). **Región Metropolitana**: Santiago, Cordillera de Las Condes, *Gunckel 21873* (CONC).

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Apéndice 1. Lista de especies e índice de colecciones numeradas. Cada especimen es citado por el apellido del primer colector en el caso en que otros coleccionistas participen de la colección. El número entre paréntesis corresponde a la especie numerada en la lista.

1. *Acaena alpina* Poepp. ex Walp.
2. *Acaena antarctica* Hook. f.
3. *Acaena argentea* Ruiz et Pav.
4. *Acaena caespitosa* Gillies ex Hook. et Arn.
5. *Acaena integerrima* Gillies ex Hook. et Arn.
6. *Acaena leptacantha* Phil.
7. *Acaena lucida* (Aiton) Vahl
8. *Acaena macrocephala* Poepp.
9. *Acaena magellanica* (Lam.) Vahl
10. *Acaena masafuerana* Bitter
11. *Acaena ovalifolia* Ruiz et Pav.
12. *Acaena patagonica* A. E. Martic.
13. *Acaena pinnatifida* Ruiz et Pav.
14. *Acaena platyacantha* Speg.
15. *Acaena poeppigiana* Gay
16. *Acaena pumila* Vahl
17. *Acaena sericea* J. Jacq.
18. *Acaena splendens* Hook. et Arn.
19. *Acaena tenera* Alboff

20a. *Acaena trifida* Ruiz et Pav.

20b. *Acaena trifida* Ruiz et Pav. var. *glabrescens* Regel et Körn.

Alboff 234 (19), s.n. (5); Andersson 280 (9); Anliot 6140 (9), 6141 (11); Arancio 10296 (9), 94201 (9); Aravena 29 (9); Arroyo 81274 (13), 81277 (1), 831286 (9), 841072 (17), 850829 (12), 850829 (12), 860084 (9), 860086 (11), 870179 (2), 870189 (12), 870202 (9), 870316 (5), 92–146 (19), 92165 (9), 92–393 (7).

Baeza 279 (18); Barrientos 1733 (13), 1761 (18); Barros s.n. (1); Beckett 4422 (9), 4471 (18); Behn s.n. (18), s.n. (20a); Borchers s.n. (13) (SGO-49838); Borge 157 (5), 214 (9); Braynshaw 202 (13), 221 (11), 246 (9); Bridges 3 (18), 4 (17), 522 (9), 772 (9), 773 (9); Buchtien 4456 (20a), 5464 (9), s.n. (13) (BREM), s.n. (9) (BREM).

Cabrera 19193 (6), 20506 (13), 23010, 23023 (13); Capt. King 10 (9), 16 (9), 46 (9), s.n. (13) (K); Carrette 215 (5); Catalán s.n. (11); Claro de la Maza s.n. (7); Commerson s.n. (16) (P-106320); Cox s.n. (9) (SGO-49832); Crawford 11863 (3).

Dessauer s.n. (11); Dollenz 207, 220, 241, 297 (9), 405 (16), 440 (9), 495, 497 (12), 918 (16), 991 (11), 1106 (16); Dombey s.n. (20a) (P-106322); Duek s.n. (8); Dusén 188 (9), 190 (9), 377 (7), 5100 (20a), 592 (6), s.n. (13) (S 8064), s.n. (3), s.n. (9) (S-R8041).

Elvebakk 34 (15), 35 (9), 470 (7), 532 (12), 537 (14), 538 (7).

Fabris 2168 (6), 784 (6); Ferruglio 49 (5); Fonk 105 (16).

Garaventa 6379 (13); Gardner 3150 (2), 3849 (9), 3889 (2), 1168 (16); Gay 527 (15), 76 (13), 78 (6), 80 (11), 81 (13), s.n. (11) (P), s.n. (9) (P-106316); Germain 88b (9), s.n. (1) (W-112652), s.n. (1) (W-110760), s.n. (1), s.n. (15), s.n. (18) (W-110770), s.n. (20a) (SGO-49930), s.n. (3), s.n. (6) (SGO-49888), s.n. (9) (K), s.n. (9) (S-8049), s.n. (9) (W-359414); Gillies 113 (5), s.n. (4); Goodall 140 (13), 191 (4), 207 (12), 2283 (9), 506 (17); Grandjot s.n. (1), s.n. (13); Gunckel 15348 (11), 15632 (11), 21873 (20b), 22508 (13), 24096 (3), 38441 (3), 50679 (5), 70058 (3); Gutiérrez 97 (6).

Headland 562 (9); Henríquez 98 (16); Hollermayer 625 (3), 712 (1); Hombron s.n. (13) (P-106302); Hooker 1827 (7), s.n. (P-106291); Hyades 901 (9).

Illin 1900 (4).

Jaffuel s.n. (1); Jiles 1585 (13), 1685 (11), 2110 (15), 4215 (9), 4438 (15), 4725 (18), 6370 (13); Junge 328 (16), s.n. (11).

Lambert s.n. (16) (UPS); Lammers 7761 (20a); Landbeck s.n. (13) (SGO-49871); Landero 671 (14), 9592 (10); Landrum 7932 (20a), 8227 (17), 8437 (4), 8446 (13); Lechler 1149 (13), 294 (13), 2951 (2), 318a (3), 584 (11), 978 (13), 978c (9); Ledezma 626 (20a), 626 (20a); Lépez 108 (3); Loyola 4 (9).

Marticorena, A. 105 (13), 135 (18), 162 (13), 228 (8), 233 (1), 272 (3), 296 (13), 297 (9), 298 (3), 299 (11), 335 (11), 421 (14), 98 (9); Marticorena, C. 106 (13), 107 (8), 1254 (5), 1417 (6), 1582 (11), 1616 (9), 1633 (11), 1949 (11), 22 (1), 429 (9), 423 (11), 599 (17), 612 (13), 81 (11), 961 (11), 1007 (9), 1019 (6); Martínez, P. 18 (11); Martínez s.n. (3); Matthei 51 (11); McSweeney 25 (2); Menzies s.n. (2); Montero 4909 (6), 4985 (6), 5277 (20a), 5490 (5), 7418 (13), 9987 (11), 10803 (20a), 12417 (13), 12648 (20a), 12649 (20a), 12650 (9); Moore 1074 (9), 2369 (9), 2499 (17), 2603 (9), 2828 (19); Moseley s.n. (3); Muñoz 6099 (9), s.n. (12).

Navas s.n. (5); Neger 4466 (20a), 4639 (6), 5099 (20a), s.n. (2), s.n. (3), s.n. (6) (M), s.n. (9) (M); Nuñez s.n. (9).

Ochsenius s.n. (9) (BREM); Ortega s.n. (17) (SGO-49831), s.n. (7) (SGO-49837).

Parra 1 (11), 168 (13); Parra, B. 476 (17); Pearce s.n. (2); Pennell 12333 (9), 12341 (15), s.n. (2); Pfister 277 (20a), 480 (11), 933 (3), 936 (13), s.n. (4), s.n. (6), s.n. (8), s.n. (9), s.n. (11), s.n. (13), s.n. (14), s.n. (19), s.n. (20a); Philippi, F. s.n. (9), s.n. (11), s.n. (18); Philippi, O., s.n. (13) (SGO-49840), s.n. (13); Philippi, R.A. 311 (3), 327 (13), 559 (9), 596a (9), s.n. (13) (SGO-49936), s.n. (13) (W-116066), s.n. (18) (W-116061), s.n. (20a), s.n. (3), s.n. (6) (SGO-49865), s.n. (6) (SGO-49905), s.n. (9) (BREM), s.n. (9) (FI), s.n. (9) (SGO-49858), s.n. (9) (SGO-49934), s.n. (9) (W-116067); Philippi s.n. (13) (M); Pinto s.n. (8); Pisano 2545 (15), 2552 (9), 2787 (17), 3106 (9), 3169 (9), 3187 (5), 3210 (9), 3301 (9), 4121, 4122 (13), 4187 (13), 4515 (17), 4531 (5), 4644 (9), 4818 (17), 4838 (11), 4969 (9), 5120 (2), 5185, 5222 (17), 5389 (16), 5494, 5521 (9), 5631 (12), 5739 (2), 5765 (9), 586 (20b), 6558 (16), 6633 (16), 6755 (13), 6782 (9), 6827 (12), 6843 (13), 6882 (2), 6901 (9), 8271-A (19), 8639 (16); Poeppig 131 (18), 45 (8), 517 (1), 684 (3).

Quezada 153 (20b), 228 (9), 373 (20b).

Reiche s.n. (20a), s.n. (3); Ricardi 219 (11), 367 (3), 693 (9), 722 (9), 966 (9), 971 (5), 1632 (9), 1662 (9), 2782 (13), 2900 (9), 3249 (18), 4096 (11), 5007 (13), 5014 (8), 5063 (9), 5232 (6), 5305 (9), 5658 (5), 5709 (8), 5735 (5), s.n. (3); Rodríguez 185 (6), 558 (20a), 843 (11), 870 (11), 1050 (11), 2083 (11), 3184 (9), 3715 (9), 4077 (16); Ruiz 10/77 (3), 10/80 (11), 10/82 (20a), 10/83 (13); Ruiz Leal 122 (17).

Saa s.n. (9), s.n. (13); Samsing s.n. (9); Savatier s.n. (9) (P-106309); Schajovskoy 94 (5); Schlegel 2318 (9), 3577 (5), 3583 (11), 7926 (20b), 8134 (19), 8197 (16); Schwabe 179

(13), 70 (2); Seki 310 (13); Silva s.n. (3); Simon 199 (18); Skottsberg 24 (7), 32 (9), 175 (9), 208 (19), 225 (16), s.n. (9) (UPS), s.n. (10) (S-R8057); Sparre 10705 (2), 10873 (5), 116 (3); Spegazzini s.n. (LP-11942, 12577); Squeo 88068 (9); Stuessy 7255 (3), 7257 (13), 7511 (13), 8443 (3), 9064 (11), 9121 (10), 9211 (10), 9214 (11), 9278 (11), 9323 (10), 9365 (10), 9416 (10), 9448 (10), 11777 (11), 15560 (6).

Taylor 1948 (18), 10380 (3), 10382 (9), 10383 (13), 10907 (13); TBPA 50 (12), 223 (9), 2397 (14), 2445 (17), 2537 (9), 2563 (12), 2638 (5), 3142 (9), 3263 (11); Tsujii 284 (13).

Valdebenito 6432 (10), 9030 (10), 9132 (10); Villagrán 6855 (2), 8176 (17); Villanueva s.n. (9); Volckmann s.n. (1); Von Bohlen 337 (13); Von Thüngen 102 (14), 17 (15).

Weldt 697 (1), 730 (11).

Zoellner 1474 (9), 5016 (20b), 5558 (6), 6476 (1), 6793 (9), 7566 (14), 10142 (18), 10379 (11).

Apéndice 2. Indice de nombres científicos. Los nombres aceptados están en **negrita** y los sinonimos en *cursivas*.

Acaena Mutis ex L.
Secc. **Acaena**
Secc. **Acrobyssinae** Bitter
Secc. *Acrocephala* Citerne
Secc. *Acrostachya* Citerne
Secc. **Ancistrum** (J. R. Forst. et G. Forst.) DC.
Secc. *Anoplocephala* Citerne
Secc. *Brachycephala* Citerne
Secc. *Elongatae* Bitter
Secc. *Euacaena* DC.
Secc. *Lachnodia* Citerne
Secc. *Microphyllae* Bitter
Secc. **Patagonicae** A. E. Martic.
Secc. **Pleurocephala** Citerne
Secc. *Pleurostachya* Citerne
Secc. *Pteracaena* Bitter
Secc. *Rhopalachanta* Bitter
Secc. **Subtuspapillosae** Bitter
acrobyssina Bitter
adscendens Vahl
var. *macrochaeta* Franch
affinis Hook. f.
alpina Poepp. ex Walp.
anserinifolia (J. R. Forst. et G. Forst.) J. Armstr.
antarctica Hook. f.
var. *laxiuscula* Bitter
argentea Ruiz et Pav.
var. *breviscapa* Bitter
var. *contracta* Bitter
var. *coriacea* Bitter
var. *grandiceps* Bitter
var. *interrupte-pinnata* Bitter
var. *lanigera* Bitter
var. *subcalvescens* Bitter
forma *epargyrea* Bitter
forma *nigricans* Bitter
forma *viridis* Bitter
cadilla Hook. f.
caespitosa Gillies ex Hook. et Arn.
calcitrapa Phil.
canescens Phil.
capitata Phil.
closiana Gay
colchaguensis Bitter
coxi Phil.
cuneata Hook. et Arn.
depauperata Bitter
digitata Phil.
var. *latifoliolata* Bitter
var. *subpinnata* Bitter
elegans Gay
elongata L.
euacantha Phil.
exaltata Bitter
fuegina Phil.
glaberrima Phil.
glandulifera Bitter
glaucella Bitter
grandistipula Bitter
grossifolia Bitter
hirsuta Phil.
hirta Citerne
humilis Bitter
integerrima Gillies ex Hook. et Arn.
var. *subpilosicupula* Bitter
ischnostemon Bitter
krausei Phil.
var. *hirsuta* (Phil.) Reiche
var. *massonandra* Bitter
var. *meionandra* Bitter
subvar. *glabratula* Bitter
laevigata W. T. Aiton var. *venulosa* (Griseb.) Reiche
leptacantha Phil.
subsp. *breviscapa* Bitter
subsp. *connectens* Bitter
subsp. *glabricupula* Bitter
subsp. *longiscapa* Bitter
var. *conferta* Bitter
var. *longissima* Bitter
var. *negeri* (E. Duse) Bitter
leptophylla Phil.
longiaristata H. Ross
longifolia Phil.
longistipula Bitter
lucida (Aiton) Vahl
lucida (Lam.) Vahl
var. *abbreviata* Bitter
var. *parvifolia* (Phil.) Reiche
var. *villosula* Bitter
macrocephala Poepp.
var. *negeri* E. Duse
macrophyes Bitter
macropoda Bitter
macrostemon Hook. f.
subsp. *closiana* (Gay) Bitter
subsp. *longiaristata* (H. Ross) Bitter
var. *basipilosa* Bitter
magellanica (Lam.) Vahl
subsp. *pygmaea* Bitter
subsp. *venulosa* (Griseb.) Bitter
var. *glabrescens* Bitter
masafuerana Bitter
micranthera Bitter
microcephala Schltdl.
multifida Hook. f.
subsp. *intercedens* Bitter
subsp. *quinquefida* Bitter
var. *utrinquepilosa* Bitter
myriophylla
neglecta Bitter
obtusiloba Bitter
oligacantha Phil.
oligoglochin Bitter
ovalifolia Ruiz et Pav.

subsp. *elegans* (Gay) Bitter
var. *elegans* (Gay) Reiche
parvifolia Phil.
patagonica A. E. Martic.
pearcei Phil.
var. *glabrinervis* Bitter
petiolulata Phil.
pinnatifida Ruiz et Pav.
subsp. *heterotricha* Bitter
subsp. *hypoleuca* Bitter
subsp. *liocarpa* Bitter
subsp. *longifolia* (Phil.) Bitter
subsp. *nudiscapa* Bitter
subsp. *oligacantha* (Phil.) Bitter
var. *calcitrapa* (Phil.) Reiche
var. *eucantha* (Phil.) Reiche
var. *intermedia* Bitter
var. *leptophylla* (Phil.) Reiche
var. *longifolia* (Phil.) Reiche
var. *macrura* Bitter
var. *oligacantha* (Phil.) Reiche
var. *parvifrons* Bitter
var. *uspallatensis* Bitter
platyacantha Speg.
plioglochin Bitter
poeppigiana Gay
pumila Phil.
pumila Vahl
var. *acrocoma* Bitter
var. *glaberrima* (Phil.) Bitter
purpureistigma Bitter
quinquefida Phil.
rubescens Bitter
sericea J. Jacq.
subsp. *subglabricupula* Bitter
var. *gracilis* Bitter
var. *sericella* Bitter
splendens Hook. et Arn.
var. *brachyphylla* Bitter
var. *breviserícea* Bitter
var. *gracilis* Bitter
var. *macrophylla* Bitter
subflaccida Bitter
tenera Alboff
subsp. *epilis* Bitter
tenuifolia Bitter
tenuipila Bitter
trifida Ruiz et Pav.
var. *argentella* Bitter
var. *brachyphylla* Bitter
var. **glabrescens** Regel et Körn.
var. *mollissima* Bitter
var. *nanodes* Bitter
var. *plurifoliolata* Bitter
var. *quinquefida* (Phil.) Reiche
var. *robusta* Bitter
var. *trifida*
triglochin Bitter
venulosa Griseb.
Ancistrum J. R. Forst. et G. Forst.
anserinifolium J. R. Forst. et G. Forst.
lucidum Aiton
lucidum Lam.
magellanicum Lam.

SCALE-DEPENDENT CLASSIFICATION OF XERIC LIMESTONE PRAIRIES: ANNUAL OR PERENNIAL GRASSLANDS?[1]

Patrick J. Lawless,[2,3] *Jerry M. Baskin,*[2] *and Carol C. Baskin*[2,4]

Abstract

Xeric limestone prairies (XLPs) are herbaceous plant communities that occur on shallow rocky calcareous soils from Missouri and Pennsylvania south to Arkansas and Georgia (U.S.A.). There has been considerable confusion regarding the classification of XLPs due to their similarity with limestone cedar glades (LCGs), an edaphic climax community type restricted to unglaciated southeastern United States. Although C_4 perennial grasses typically are the dominant taxa in XLPs, portions of sites with extremely shallow soils (≤ 0.1 m) are typified by local dominance of *Sporobolus vaginiflorus* (Torr. ex Gray) Alf. Wood, a C_4 summer annual grass that is the characteristic dominant in LCGs. In this study, we assess the relative importance of C_4 perennial grasses versus *S. vaginiflorus* in XLP community types identified in Kentucky over a range of scales. We then use these data to analyze variability in XLP vegetation and physical environmental conditions and to further compare XLPs with LCGs. *Sporobolus vaginiflorus* had high frequencies in many of the fine-scale community types (0.01 and 0.1 m^2) identified in this study. However, dominance of C_4 perennial grasses (particularly *Schizachyrium scoparium* (Michx.) Nash) in all 12 of the community types identified at the largest scale (100 m^2) is indicative of the relatively small areal extent of extremely shallow-soiled regions in XLPs. XLPs also differ from LCGs in that the former generally lack early-stage primary successional community types dominated by cryptograms and/or C_3 annual forbs. Thus, the results of our study suggest that the total range of environmental conditions and the variety and extent of plant community types present in a site should be considered when classifying the vegetation of calcareous rock outcrop communities in the eastern United States.

Key words: cedar glades, community classification, rock outcrop, scale, xeric limestone prairies.

Herbaceous plant communities developed on shallow rocky calcareous soils are broadly distributed in the Eastern Deciduous Forest region (sensu Braun, 1950) in the eastern United States. As is the case in many other types of rock outcrop vegetation, species composition and fine-scale structure in calcareous rock outcrop communities are strongly dependent on local physical environmental conditions, particularly soil depth (e.g., Quarterman, 1948; Skinner, 1979; Somers et al., 1986; Ver Hoef et al., 1993; Rollins, 1997; Baskin & Baskin, 1999). Consequently, classification and description of these plant communities may be affected significantly by the scale at which community sampling is conducted and the heterogeneity of physical environmental conditions within sites. In this study, we consider the effect(s) of grain (i.e., quadrat size) on the classification of species-rich calcareous grasslands known as xeric limestone prairies (XLPs) (sensu Baskin et al., 1994; Baskin & Baskin, 2000; Lawless, 2005).

XLPs are distributed from Missouri (Nelson & Ladd, 1983; Baskin & Baskin, 2000) and Pennsylvania (Laughlin & Uhl, 2003) south to Arkansas (Keeland, 1978; Baskin & Baskin, 2000) and Georgia (DeSelm, 1993). Baskin et al. (1994) and Baskin and Baskin (2000) described these herbaceous communities as C_4 perennial grasslands dominated by *Schizachyrium scoparium* (Michx.) Nash and/or *Bouteloua curtipendula* Torr. However, transitions in dominance from C_4 perennial prairie grasses (*S. scoparium*, *Sorghastrum nutans* (L.) Nash, *Andropogon gerardii* Vitman, and *B. curtipendula*) to C_4 annual grasses (*Sporobolus* R. Br. spp.) often occur in response to decreased soil depths (Ver Hoef et al., 1993; Baskin & Baskin, 2000; Rhoades et al., 2004). Dominance of *Sporobolus vaginiflorus* (Torr. ex Gray) Alf. Wood in the shallow-soil regions of some XLP sites has resulted in confusion of this vegetation type with limestone cedar glades (LCGs) (sensu Baskin & Baskin, 1999, 2000, 2003, 2004), an edaphic climax vegetation type in which the C_4 annual grass *S. vaginiflorus* is the characteristic dominant (Quarterman, 1948; Somers et al., 1986; Rollins, 1997; Baskin & Baskin, 1999).

In this study, we determined the effect of grain on the classification and description of XLP vegetation in

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the Interior Plateau ecoregion in Kentucky (sensu Woods et al., 2002). We assess the relative importance of C_4 perennial grass species versus *Sporobolus vaginiflorus* in XLP community types identified in this study for comparison with XLP and LCG community types described in other studies. Additional biotic variables and physical environmental conditions also are considered as potential sources of variability within and among XLP sites and between XLPs and LCGs. Our research affords insight into the primary source(s) of variability within and among XLPs and identifies key compositional and structural differences between XLPs and LCGs, thus facilitating classification of these vegetation types.

This study focused on XLPs in Kentucky, because (1) numerous XLP sites occur in the state, (2) many of these XLPs are owned and/or managed by state agencies and/or conservation organizations, thus affording relatively easy access, and (3) quantitative vegetation data are lacking for the vast majority of sites in the state. It should also be noted that the presence of both XLPs and LCGs in Kentucky has resulted in considerable confusion regarding the classification of herbaceous vegetation associated with calcareous rock outcrops in this area (Baskin et al., 1994).

Methods

Sampling

In July through October of 2002 and 2003, the vegetation of 18 XLPs in the Interior Plateau ecoregion in Kentucky (see Table 1 for sample site locations) was sampled using a nested quadrat sampling design adapted from Peet et al. (1998) (0.01-, 0.1-, 1-, 10-, and 100-m^2 quadrats). Presence of all nonwoody vascular plant species was recorded in the 0.01- to 10-m^2 quadrats. Each taxon present in the largest quadrat (100-m^2 sampling module) was assigned to one of 10 cover classes. Soil depth was recorded to the nearest centimeter in the four corners of all modules, and soil samples were collected from the top 25 cm of soil in the same locations. Soil samples from each module were composited and submitted to the University of Kentucky Soil Testing Laboratory for the following analyses: pH, buffered pH, texture, water holding capacity, percent organic matter, total nitrogen, cation exchange capacity (total and individually for K, Ca, Mg, and Na), base saturation, and concentrations of P, K, Ca, Mg, Zn, Cu, Mn, Na, Fe, and Al. Three measurements of slope (%) and aspect of slope (in degrees east of true north) were collected for each module using a compass and clinometer, respectively, and an average was calculated for each parameter. The average aspect of slope (Φ) for each module then was used to calculate a corresponding heat load index (HLI) using the following equation: $HLI = (1 - \cos(\Phi - 45))/2$.

Table 1. County and ecoregional locations of the 18 xeric limestone prairies sampled in Kentucky. Ecoregions follow Level IV ecoregions of the Interior Plateau (Level III ecoregion; sensu Woods et al., 2002).

	Site	County	Ecoregion
1	Fort Knox Military Reservation 1	Hardin	Knobs-Norman Upland
2	Fort Knox Military Reservation 2	Hardin	Knobs-Norman Upland
3	Cedar Creek Farms	Hardin	Knobs-Norman Upland
4	Scudder Glade	Hardin	Knobs-Norman Upland
5	Hardin Co. Cedar Glade	Hardin	Knobs-Norman Upland
6	Muldraugh's Barren	Hardin	Knobs-Norman Upland
7	Mixed Grass Barrens	Larue	Knobs-Norman Upland
8	Spalding Glade	Larue	Knobs-Norman Upland
9	Thompson Creek Glade	Larue	Knobs-Norman Upland
10	Pine Creek Barrens	Bullitt	Outer Bluegrass
11	Crooked Creek Barrens 1	Lewis	Outer Bluegrass
12	Crooked Creek Barrens 2	Lewis	Outer Bluegrass
13	Grayson Co. Barren	Grayson	Crawford-Mammoth Cave Uplands
14	Knight's Barren	Hardin	Crawford-Mammoth Cave Uplands
15	Lapland Barrens	Meade	Crawford-Mammoth Cave Uplands
16	Lapland Road Barrens	Meade	Crawford-Mammoth Cave Uplands
17	Logan Co. Glade	Logan	Western Pennyroyal Karst Plain
18	Logan Co. Barrens	Logan	Western Pennyroyal Karst Plain

Classification and Ordination

The flexible beta linkage agglomerative clustering method in PC-ORD (MJM Software Design; McCune & Mefford, 1999) was used to identify community types over the range of spatial scales sampled. A beta value of −0.25 and Sorensen's distance measure were used in all analyses. Indicator species analysis was used to determine the optimal number of groups at each scale via selection of the group number with the lowest average P value (Dufrêne and Legendre, 1997).

Nonmetric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976) was used to determine variability in community structure at the 100-m^2 scale and to investigate potential sources of variability. A random starting configuration and Sorensen's distance measure were used in the analysis of ground-layer cover class data, which included 40 runs with real data and 50 runs with randomized data (PC-ORD; MJM Software Design; McCune & Mefford, 1999). Abiotic environmental data and cover class data from the primary matrix were entered into a second matrix for calculation of coefficients of determination (r^2) with ordination axes. Only variables with an r^2 value greater than or equal to 0.35 were included in joint plots.

Results

Cluster analysis

0.01-m^2 Community types

Of 174 0.01-m^2 quadrats sampled, 159 contained one or more individuals and were included in cluster analysis. Four community types were identified at the 0.01-m^2 scale, and percent occurrence data resulted in only four characteristic taxa (% occurrence ≥ 30), all of which are graminoids (see summary of characteristic taxa in Table 2) (full analysis of community types at each of five scales is available from the authors by request). Three taxa, *Schizachyrium scoparium*, *Sporobolus vaginiflorus*, and *Carex crawei* Dewey ex Torr., were characteristic in two community types, and *Sorghastrum nutans* was a characteristic taxon in a single community type. The *S. scoparium–S. vaginiflorus* community type contained more quadrats (48) and occurred in more sites (15) than any other community type. The *S. vaginiflorus–C. crawei* community type contained 46 quadrats and occurred in 14 of 18 sites. The community type present in the smallest number of sites (8) and quadrats (22) supported no characteristic taxa.

0.1-m^2 Community types

Of 174 0.1-m^2 quadrats, 173 contained one or more individuals and were included in cluster analysis. Ten community types were identified at the 0.1-m^2 scale, and percent occurrence data resulted in a total of 19 characteristic taxa (% occurrence ≥ 40) among these community types. *Schizachyrium scoparium* was a characteristic taxon in six of these community types, more than any other taxon, and was followed by *Sporobolus vaginiflorus* (4) and *Carex crawei* (3). Eight taxa had a percent occurrence greater than or equal to all other taxa in one or more community types, including *S. scoparium* (4 community types), *S. vaginiflorus* (2), *Andropogon gerardii* (1), *Sorghastrum nutans* (1), *C. meadii* Dewey (1), *C. crawei* (1), *Ruellia humilis* Nutt. (1), and *Rosa carolina* L. (1). The *S. scoparium–S. vaginiflorus–Echinacea simulata* McGregor–*Hedyotis nigricans* (Lam.) Fosberg community type and the *S. vaginiflorus–Heliotropium tenellum* Torr.–*Hypericum dolabriforme* Vent. community type occurred in the largest number of sites (9). The *C. crawei–S. scoparium–S. vaginiflorus–R. humilis* community type was represented in the largest number of quadrats (40).

1-m^2 Community types

All 174 of the 1-m^2 quadrats sampled contained one or more individuals and were included in cluster analysis. Ten community types were identified at the 1-m^2 scale, and percent occurrence data resulted in a total of 39 characteristic taxa (% occurrence ≥ 50) among these community types. *Schizachyrium scoparium* was a characteristic taxon in nine of 10 community types and was followed by *Sporobolus vaginiflorus* (6 community types), *Echinacea simulata* (5), *Euphorbia corollata* L. (5), *Physostegia virginiana* Benth. (5), *Sorghastrum nutans* (4), and *Ruellia humilis* (4). *Schizachyrium scoparium* had a percent occurrence greater than or equal to all taxa in five community types. Other taxa with a percent occurrence greater than or equal to all taxa in two or more community types included *E. simulata* (4 community types) and *S. vaginiflorus* (2). The *S. scoparium–E. simulata–S. vaginiflorus* community type occurred in the most sites (8) and was represented in the largest number of quadrats (51).

10-m^2 Community types

Twelve community types were identified at the 10-m^2 scale, and percent occurrence data resulted in a total of 73 characteristic taxa (% occurrence ≥ 60) among these community types. *Schizachyrium scoparium* was a characteristic taxon in all 12 community types. Only eight additional taxa were characteristic in seven or more community types, including *Sporobolus vaginiflorus* (8), *Sorghastrum nutans* (8), *Echinacea simulata* (8), *Physostegia virginiana* (8), *Euphorbia corollata* (8), *Ruellia humilis* (7), *Solidago nemoralis* Aiton (7), and *Juniperus virginiana* L. (7). *Schizachyrium scoparium* had a percent occurrence greater than or equal to all other taxa in 8 community types and was followed by *S. vaginiflorus* (4) and *E. simulata* (4). The *S. scoparium–S. nutans–E. simulata–S. vaginiflorus* community type occurred in five sites in the Knobs-Norman Upland ecoregion and was represented in more quadrats (36) than any other community type.

Table 2. Summary of characteristic taxa identified at all five spatial scales (0.01–100 m^2) in XLPs in Kentucky, U.S.A. Taxonomy is in accordance with the United States Department of Agriculture, Natural Resources Conservation Service (2004). All voucher specimens were collected in Kentucky and are deposited at KY. Site localities are in accordance with site numbers listed in Table 1.

Family	Species	Site locale	Date	Specimen ID
Acanthaceae	*Ruellia humilis* Nutt.	17	3 July 2002	*Patrick Lawless s.n.*
Agavaceae	*Manfreda virginica* Salisb.	17	3 July 2002	*Patrick Lawless s.n.*
Alliaceae	*Allium cernuum* Roth	1	25 Aug. 2003	*Patrick Lawless s.n.*
Anacardiaceae	*Rhus aromatica* Aiton	10	14 June 2002	*Patrick Lawless s.n.*
Apocynaceae	*Apocynum cannabinum* L.	4	10 July 2002	*Patrick Lawless s.n.*
Asclepiadaceae	*Asclepias viridiflora* Raf.	8	11 Aug. 2003	*Patrick Lawless s.n.*
Asteraceae	*Ambrosia artemisiifolia* L.	13	26 Aug. 2002	*Patrick Lawless s.n.*
	Brickellia eupatorioides (L.) Shinners	17	3 July 2002	*Patrick Lawless s.n.*
	Coreopsis tripteris L.	17	10 July 2002	*Patrick Lawless s.n.*
	Echinacea simulata McGregor	17	5 July 2002	*Patrick Lawless s.n.*
	Eupatorium altissimum L.	17	3 July 2002	*Patrick Lawless s.n.*
	Helianthus hirsutus Raf.	4	10 July 2002	*Patrick Lawless s.n.*
	Liatris aspera Michx.	4	10 July 2002	*Patrick Lawless s.n.*
	Liatris cylindracea Michx.	11	25 July 2002	*Patrick Lawless s.n.*
	Liatris squarrosa Michx.	10	14 June 2002	*Patrick Lawless s.n.*
	Liatris squarrulosa Michx.	10	20 Sep. 1991	*Barry Dalton s.n.*
	Oligoneuron rigidum var. *glabratum* (E. L. Braun) G. L. Nesom	4	10 July 2002	*Patrick Lawless s.n.*
	Parthenium integrifolium L.	4	10 July 2002	*Patrick Lawless s.n.*
	Silphium pinnatifidum Elliott	9	7 Aug. 2003	*Patrick Lawless s.n.*
	Silphium terebinthinaceum Jacq.	11	25 June 2002	*Patrick Lawless s.n.*
	Silphium trifoliatum L.	14	28 July 1978	*Ray Cranfill s.n.*
	Solidago nemoralis Aiton	5	29 Sep. 2003	*Patrick Lawless s.n.*
	Symphyotrichum laeve (L.) A. Löve & D. Löve	4	10 July 2002	*Patrick Lawless s.n.*
	Symphyotrichum urophyllum (DC.) G. L. Nesom	4	10 July 2002	*Patrick Lawless s.n.*
Boraginaceae	*Heliotropium tenellum* Torr.	17	3 July 2002	*Patrick Lawless s.n.*
	Lithospermuan canescens Lehm.	17	3 July 2002	*Patrick Lawless s.n.*
Caesalpiniaceae	*Cercis canadensis* L.	6	22 Sep. 2002	*Patrick Lawless s.n.*
Campanulaceae	*Lobelia spicata* Lam.	17	5 July 2002	*Patrick Lawless s.n.*
Clusiaceae	*Hypericum dolabriforme* Vent.	17	3 July 2002	*Patrick Lawless s.n.*
Cornaceae	*Cornus drummondii* C. A. Mey.	12	26 July 2002	*Patrick Lawless s.n.*
Cupressaceae	*Juniperus virginiana* L.	6	22 Sep. 2002	*Patrick Lawless s.n.*
Cyperaceae	*Carex crawei* Dewey ex Torr.	6	19 May 2002	*Patrick Lawless s.n.*
	Carex meadii Dewey	17	3 July 2002	*Patrick Lawless s.n.*
	Carex umbellata Schkuhr	6	19 May 2002	*Patrick Lawless s.n.*
	Fimbristylis puberula (Michx.) Vahl	10	14 June 2002	*Patrick Lawless s.n.*
Ebenaceae	*Diospyros virginiana* L.	13	26 Aug. 2002	*Patrick Lawless s.n.*
Euphorbiaceae	*Croton capitatus* Michx.	9	13 June 2002	*Patrick Lawless s.n.*
	Croton monanthogynus Michx.	4	10 July 2002	*Patrick Lawless s.n.*
	Euphorbia corollata L.	10	14 June 2002	*Patrick Lawless s.n.*
Fabaceae	*Desmodium glabellum* DC.	11	25 July 2002	*Patrick Lawless s.n.*
	Galactia volubilis (L.) Britton	17	7 July 2002	*Patrick Lawless s.n.*
	Lespedeza virginica (L.) Britton	17	3 July 2002	*Patrick Lawless s.n.*
	Melilotus alba Medik.	11	3 July 2002	*Patrick Lawless s.n.*
Gentianaceae	*Sabatia angularis* (L.) Pursh	4	10 July 2002	*Patrick Lawless s.n.*
Iridaceae	*Sisyrinchium albidum* Raf.	4	10 July 2002	*Patrick Lawless s.n.*
Lamiaceae	*Blephilia ciliata* Raf.	10	14 June 2002	*Patrick Lawless s.n.*
	Isanthus brachiatus Britton, Sterns & Poggenb.	4	10 July 2002	*Patrick Lawless s.n.*
	Monarda fistulosa L.	17	5 July 2002	*Patrick Lawless s.n.*

Table 2. Continued.

Family	Species	Site locale	Date	Specimen ID
	Physostegia virginiana Benth.	5	6 Aug. 2003	*Patrick Lawless s.n.*
	Pycnanthemum tenuifolium Schrad.	17	5 July 2002	*Patrick Lawless s.n.*
Linaceae	*Linum sulcatum* Riddell	17	3 July 2002	*Patrick Lawless s.n.*
Oleaceae	*Fraxinus americana* L.	13	3 June 2002	*Patrick Lawless s.n.*
Onagraceae	*Gaura filipes* Spach	4	10 July 2002	*Patrick Lawless s.n.*
Poaceae	*Andropogon gerardii* Vitman	4	10 July 2002	*Patrick Lawless s.n.*
	Aristida purpurascens Poir.	10	—	*Julian Campbell s.n.*
	Bouteloua curtipendula Torr.	17	3 July 2002	*Patrick Lawless s.n.*
	Danthonia spicata (L.) P. Beauv. ex Roem. & Schult.	4	18 June 2003	*Rob Paratley s.n.*
	Dichanthelium acuminatum (Sw.) Gould & C. A. Clark	9	13 June 2002	*Patrick Lawless s.n.*
	Dichanthelium sphaerocarpon (Ellis) Gould	17	3 July 2002	*Patrick Lawless s.n.*
	Panicum flexile (Gattinger) Scribn.	4	10 July 2002	*Patrick Lawless s.n.*
	Schizachyrium scoparium (Michx.) Nash	4	10 July 2002	*Patrick Lawless s.n.*
	Sorghastrum nutans (L.) Nash	4	10 July 2002	*Patrick Lawless s.n.*
	Sporobolus compositus Merr.	17	7 July 2002	*Patrick Lawless s.n.*
	Sporobolus vaginiflorus (Torr. ex Gray) Alf. Wood	4	10 July 2002	*Patrick Lawless s.n.*
Polygalaceae	*Polygala verticillata* L.	17	3 July 2002	*Patrick Lawless s.n.*
Ranunculaceae	*Clematis pitcheri* Torr. & A. Gray	17	5 July 2002	*Patrick Lawless s.n.*
Rosaceae	*Potentilla simplex* Michx.	17	5 July 2002	*Patrick Lawless s.n.*
	Rosa carolina L.	14	26 June 1992	*Julian Campbell s.n.*
Rubiaceae	*Galium circaezans* Michx.	4	10 July 2002	*Patrick Lawless s.n.*
	Hedyotis nigricans (Lam.) Fosberg	4	10 July 2002	*Patrick Lawless s.n.*
	Houstonia canadensis Willd. ex Roem. & Schult.	17	3 July 2002	*Patrick Lawless s.n.*
Santalaceae	*Comandra umbellata* Nutt.	10	14 June 2002	*Patrick Lawless s.n.*
Scrophulariaceae	*Agalinis tenuifolia* Raf.	10	8 Sep. 1992	*Julian Campbell s.n.*
	Castilleja coccinea Spreng.	12	25 July 2002	*Patrick Lawless s.n.*
Smilacaceae	*Smilax bona-nox* L.	17	3 July 2002	*Patrick Lawless s.n.*
Ulmaceae	*Celtis tenuifolia* Nutt.	17	3 July 2002	*Patrick Lawless s.n.*
Violaceae	*Viola pedata* L.	17	3 July 2002	*Patrick Lawless s.n.*

100-m² Community types

Forty-one taxa had an average cover value of 3% or greater in one or more community types. Fifteen taxa were dominant (avg. cover $\geq$ 10%) in one or more community type(s). Six of these 15 taxa were dominant in three or more community types, including *Schizachyrium scoparium* (10 community types), *Sporobolus vaginiflorus* (5), *Sorghastrum nutans* (5), *Echinacea simulata* (5), *Andropogon gerardii* (4), and *Carex crawei* (3). *Schizachyrium scoparium* had the highest average cover in 10 of 12 community types identified in this study and in 20 of 22 other studies of XLPs in the eastern United States for which vegetation data were available (Table 3). *Andropogon gerardii* and *Silphium terebinthinaceum* Jacq. each had the highest cover in one 100-m² community type. *Schizachyrium scoparium* and *S. vaginiflorus* were co-dominant in five of 12 community types, and *S. scoparium* and *S. nutans* were co-dominant in four of 12 community types. Only seven taxa were subdominant in three or more community types. *Andropogon gerardii* was subdominant in seven community types, and six taxa, including *E. simulata*, *C. meadii*, *Hedyotis nigricans*, *S. nutans*, *Juniperus virginiana*, and *Cercis canadensis* L., each were subdominant in three community types.

ORDINATION

Monte Carlo test results were statistically significant ($P \leq 0.02$) for each of the six ordination axes analyzed. The final NMS ordination consisted of 400 iterations of a three-dimensional solution and resulted in final stress equal to 15.33 and instability equal to 0.00829. Percent of variance (equal to cumulative r^2 $\times$ 100) collectively explained by the three axes was

Table 3. Summary of dominant taxa in XLPs of the eastern United States. Data (quantitative and qualitative) are organized by Level III ecoregions (sensu Omernik, 1987).

Ecoregion	Dominant taxon	Reference	Data
Ozark Highlands	*Sporobolus neglectus**	Hall, 1955	frequency
	Schizachyrium scoparium	Kucera & Martin, 1957	avg. cover
	Schizachyrium scoparium	Keeland, 1978	avg. cover
	Schizachyrium scoparium†	Skinner, 1979	avg. frequency
	Sporobolus neglectus‡	Skinner, 1979	avg. frequency
	Schizachyrium scoparium	Hicks, 1981	avg. importance value
	Schizachyrium scoparium	Logan, 1992	semi-quantitative
	Schizachyrium scoparium	Ver Hoef et al., 1993	avg. geometric mean of cover
	*Panicum virgatum**	George, 1996	avg. cover
	Schizachyrium scoparium	George, 1996	avg. cover
Eastern Corn Belt Plains	*Schizachyrium scoparium*	Maxwell, 1987	qualitative
Interior River Hills and Lowlands	*Schizachyrium scoparium*	McClain & Ebinger, 2002	avg. cover
	Bouteloua curtipendula	McClain & Ebinger, 2002	avg. cover
	Hedyotis nigricans	McClain & Ebinger, 2002	avg. cover
	Schizachyrium scoparium	Heikens, 1991	avg. cover
Interior Plateau	*Schizachyrium scoparium*	Heikens, 1991	avg. cover
	Silphium terebinthinaceum	Heikens, 1991	avg. cover
	*Schizachyrium scoparium***	Kurz, 1981	avg. frequency
	Schizachyrium scoparium	Braun, 1928	avg. frequency
	Andropogon gerardii	Braun, 1928	avg. frequency
	Schizachyrium scoparium	Baskin & Baskin, 1977	frequency
	Schizachyrium scoparium	DeSelm, 1988	importance values
	Schizachyrium scoparium	DeSelm, 1991	avg. cover
	Schizachyrium scoparium	DeSelm & Webb, 1997	avg. cover
	*Sporobolus clandestinus**	DeSelm & Webb, 1997	avg. cover
	Schizachyrium scoparium	this study	avg. cover
	Andropogon gerardii	this study	avg. cover
	Silphium terebinthinaceum	this study	avg. cover
Ridge and Valley	*Bouteloua curtipendula*	Bartgis, 1993	avg. cover
	Solidago arguta var. *harrisii**	Bartgis, 1993	qualitative
	Monarda fistulosa var. *brevis**	Bartgis, 1993	qualitative
	*Paronychia virginica**	Bartgis, 1993	qualitative
	Schizachyrium scoparium	DeSelm, 1993	avg. cover
	Andropogon gerardii	DeSelm, 1993	avg. cover
	Schizachyrium scoparium	Ludwig, 1999	avg. cover
	Andropogon gerardii	Ludwig, 1999	avg. cover
	Schizachyrium scoparium	Allison & Stevens, 2001	qualitative
	Bouteloua curtipendula	Laughlin & Uhl, 2003	semi-quantitative
Southeastern Plains	*Schizachryium scoparium*	Harper, 1920	qualitative

* Authors and families of taxa that are in this table but do not appear in Table 2 are as follows: *Sporobolus neglectus* Nash (Poaceae), *Panicum virgatum* L. (Poaceae), *Sporobolus clandestinus* Hitchcock (Poaceae), *Solidago arguta* Spreng. var. *harrisii* (E. S. Steele) A. W. Cusick (Asteraceae), *Monarda fistulosa* var. *brevis* Fosber & Artz (Lamiaceae), *Paronychia virginica* L. (Caryophyllaceae).

† Based on frequency data collected in 0.01 and 0.1-m^2 quadrats centered around the rare focal species *Stenosiphon linifolius* (Nutt. ex E. James) Heynh. (Onagraceae).

‡ Based on frequency data collected in 0.01 and 0.1-m^2 quadrats centered around the rare focal species *Penstemon cobaea* var. *purpureus* Pennell (Scrophulariaceae) and *Centaurium texense* (Griseb.) Fernald (Asteraceae).

** Twenty-three of 32 sample sites were located in the Interior Plateau and nine in the Ozark Highlands; however, data were not stratified by site.

82.9%, and the increment r^2 values of the three axes were as follows: 1 = 0.234, 2 = 0.226, and 3 = 0.369. Orthogonality between axis pairs ranged from 97.2% to 99.1%.

Only quadrats from the two sites in the eastern Outer Bluegrass ecoregion (Crooked Creek Barrens sites 1 and 2) had relatively large negative eigenvectors (~ −1) on axis three (Fig. 1), and as a result the

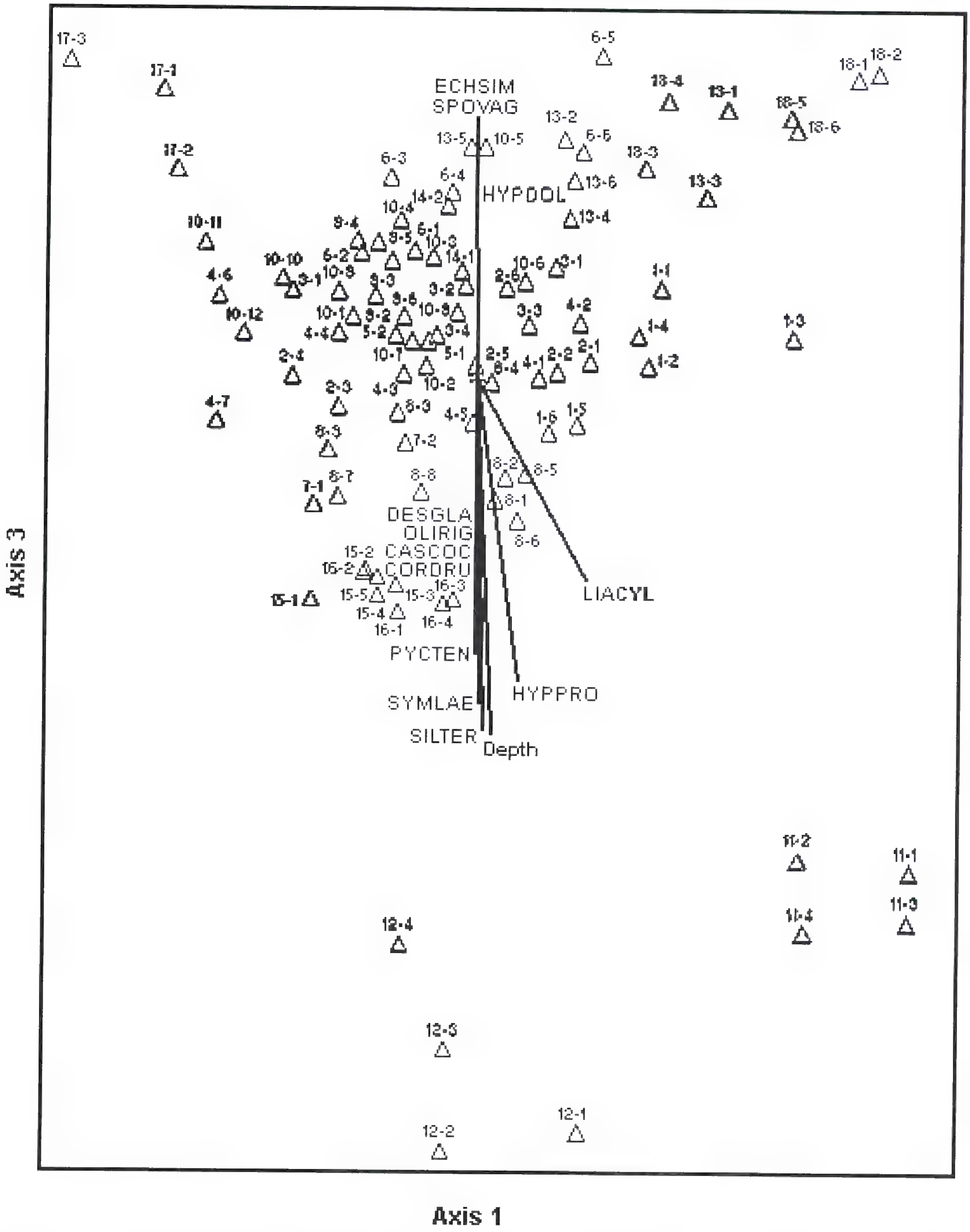

Figure 1. Joint plot (axis 1 vs. 3) including abiotic environmental variables and taxa with r^2 values greater than or equal to 0.35. Each 100-m² quadrat (i.e., sample module) is represented by a triangle labeled with site number (from Table 1) followed by module number within site. Taxon codes are formed by the first three letters of the genus and species epithet, respectively. "Depth" symbolizes soil depth.

distances between these quadrats and all others were high. There was a strong negative correlation between soil depth and axis three, and cover of 11 taxa also was correlated (r^2 value ≥ 0.35) with axis three. Cover of *Silphium terebinthinaceum*, *Symphyotrichum laeve* (L.) A. Löve & D. Löve, *Hypericum prolificum* L., *Pycnanthemum tenuifolium* Schrad., *Liatris cylindracea* Michx., *Cornus drummondii* C. A. Mey., *Castilleja*

coccinea Spreng., *Oligoneuron rigidum* var. *glabratum* (E. L Braun) G. L. Nesom, and *Desmodium glabellum* DC. was correlated negatively with axis three, and cover of *Sporobolus vaginiflorus* and *Echinacea simulata* was correlated positively with this axis. Axis three eigenvectors of quadrats from Logan County Glade and Logan County Barrens were large (≥ 0.59). Only quadrats from Pine Creek Barrens had relatively large positive eigenvectors (≥ 0.6) on axis two. Cover of *Carex crawei*, *Aristida purpurascens* Poir., *Euphorbia corollata*, *Symphotrichum urophyllum* (DC.) G. L. Nesom, and *L. squarrosa* Michx. was correlated positively with axis two.

Discussion

Results of this study confirm that XLPs in Kentucky are C_4 perennial grasslands as described by Baskin et al. (1994) and Baskin and Baskin (2000). Despite *Sporobolus vaginiflorus* being a dominant taxon (avg. cover ≥ 10%) in five of 12 100-m^2 community types, collective average cover of C_4 perennial grasses (primarily *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Andropogon gerardii*) exceeded cover of *S. vaginiflorus* in all 12 100-m^2 community types. *Schizachyrium scoparium* had the highest average cover in 10 of 12 100-m^2 XLP community types identified in this study and was dominant (i.e., had the highest cover, frequency, or importance value) in 17 of 19 studies conducted in XLPs in other regions of the eastern United States. Thus, *S. scoparium* should be considered the characteristic dominant taxon in XLPs of the eastern United States.

However, *Sporobolus vaginiflorus* was a characteristic taxon in the majority of community types identified in this study at scales less than 100 m^2. In one of four 0.01-m^2 community types and two of 10 0.1-m^2 community types, *S. vaginiflorus* was the only characteristic grass taxon, thus indicating local dominance of this taxon in a considerable number of sites. This finding is consistent with those of Hall (1955), Kucera and Martin (1957), Skinner (1979), Hicks (1981), Nelson (1985), Logan (1992), and Ver Hoef et al. (1993) on XLPs in the Ozarks, which were summarized by Baskin and Baskin (2000). Therefore, when considered at fine spatial scales, portions of some XLP sites fit the physiognomic description of cedar glades provided by Baskin and Baskin (2003).

Sporobolus vaginiflorus and *Schizachyrium scoparium* were both characteristic in the 0.01-m^2 and 0.1-m^2 community types identified in this study that contained the largest number of quadrats. Therefore, *S. vaginiflorus* is not necessarily confined to portions of sites in which perennial grasses are absent, which typically have extremely shallow (≤ 0.1 m) soil depths, and apparently is capable of competing with these grasses over a range of local environmental conditions. Frequencies of both *S. vaginiflorus* and C_4 perennial grasses (*Bouteloua curtipendula* and/or *Sorghastrum nutans*) also were high in the shallow-soil community types ("rocky glade" and "shallow soil glade") on Gasconade Dolomite described by Ver Hoef et al. (1993). In addition, high frequency of co-occurrence of *S. vaginiflorus* and *Andropogon virginicus* L./*S. scoparium* (uncertainty resulting from spring sampling) was observed in one of the 14 0.1-m^2 LCG community types identified by Rollins (1997).

In the XLPs sampled in Kentucky, soil depth and *Sporobolus vaginiflorus* cover also were significant sources of variability at the largest grain (100 m^2). However, 13 of the 17 taxa with r^2 values greater than or equal to 0.35 were herbs. This phenomenon is due largely to the small number of characteristic graminoid taxa and their high percent occurrence values in this vegetation type. Thus, the patchy distribution of herbaceous taxa is largely responsible for differences in species composition among sites, because the dominant graminoids are present in the vast majority of sites. This patchy distribution pattern most likely is attributable to the rarity of this vegetation type at the landscape scale and small area of XLPs in comparison with the regionally dominant deciduous forests and agricultural lands (Lawless et al., 2004). Therefore, colonization, extinction, and factors that affect such processes (e.g., site area, distance from nearest site, regional species pools) strongly influence species composition in XLPs and are primary sources of variability in this vegetation type throughout its range in the eastern United States.

Comparison of XLPs and LCGs and their classification

The C_4 annual grass *Sporobolus vaginiflorus* is an important component of both XLP and LCG community types. In XLPs, *S. vaginiflorus* is locally dominant in areas with extremely shallow soils (≤ 0.1 m), and it is abundant in areas of greater soil depth, where *Schizachyrium scoparium* (or other C_4 perennial grasses) is the dominant taxon. Lack of dominance of *S. vaginiflorus* in any of the 12 100-m^2 community types identified in this study suggests that extremely shallow soils are not areally extensive in XLPs. Conversely, dominance of *S. vaginiflorus* in LCG community types identified over a range of scales, from 0.01 to 100 m^2 (Quarterman, 1948; Somers et al., 1986; Rollins, 1997), is indicative of the pervasiveness of extremely shallow soils in the LCG vegetation type. Therefore, average soil depth and the range of soil depths in XLPs and LCGs are considerably different.

XLPs and LCGs differ not only with respect to their characteristic dominant taxa and soil depth characteristics but also in the different community types that occur in each kind of vegetation and in the species composition of these community types. Although mosses, lichens, blue-green algae (*Nostoc commune* Vaucher), and macrobiotic crusts were observed in some sites sampled in this study, they were not observed in high frequency. Conversely, early-stage primary successional community types dominated by cryptograms are common in LCGs (Quarterman, 1948; Somers et al., 1986; Rollins, 1997; Baskin & Baskin, 1999), as well as many other rock outcrop vegetation types in the eastern United States, including alvars (Catling & Brownell, 1999), granite rock outcrops (Oosting & Anderson, 1939; Burbanck & Platt, 1964; Shure & Ragsdale, 1977; Shure, 1999), sandstone rock outcrops (Perkins, 1981), rock ledges (Winterringer & Vestal, 1956), and high-elevation rock outcrops of various substrates (Wiser & White, 1999). In addition, XLPs generally lack the C_3 annual forb-dominated seral stages that typically occur in LCGs subsequent to soil genesis by cryptogram community types (Quarterman, 1948; Somers et al., 1986; Rollins, 1997; Baskin & Baskin, 1999). These C_3 annual forb-dominated community types are restricted to areas of LCGs with very thin soils over bedrock, and they are the primary habitat for a considerable number of taxa (e.g., *Leavenworthia* Torr. spp.) endemic or near endemic to LCGs of the southeastern United States (sensu Baskin & Baskin, 1999, 2003). Thus, absence or infrequency of these physical environmental conditions and corresponding C_3 annual forb-dominated community types in XLPs may explain the low frequency of occurrence of LCG endemics and/or near endemics in XLPs of the eastern United States (Lawless, 2005).

Community types identified in this study represent compositional and structural variation within and among XLP plant communities. Some XLP community types identified in this study and in others (particularly those dominated by *Sporobolus vaginiflorus*) closely resemble those present in LCGs of the southeastern United States. However, distinct differences are apparent between XLPs and LCGs when the total range of environmental conditions and the variety and extent of plant community types present are considered. Prevalence of C_4 perennial grass–dominated community types, infrequency or absence of early stage primary successional seres composed of cryptograms and/or C_3 annual forbs, and extremely variable soil depths (< 0.01 to > 1 m) are all characteristics of XLPs that distinguish them from LCGs and, thus, should be used in any classification system involving these calcareous rock outcrop vegetation types.

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POLLINATION BIOLOGY IN A TROPICAL HIGH-ALTITUDE GRASSLAND IN BRAZIL: INTERACTIONS AT THE COMMUNITY LEVEL[1,2]

Leandro Freitas[3] *and Marlies Sazima*[4]

Abstract

Surveys of local assemblages of plants and their pollinators are among the most useful ways to evaluate specialization in pollination and to discuss the patterns of plant-pollinator interactions among ecosystems. The high-altitude grasslands from southeastern Brazil constitute diminutive island-like formations surrounded by montane rainforests. We registered the floral traits of 124 species from the Serra da Bocaina grasslands (about 60% of the animal-pollinated species of this flora), and determined the pollinators of 106 of them. Asteraceae (40 species) and Melastomataceae (10 species) were prominent, while most families were represented by few species. The predominant floral traits were: dish or short-tubular shape; nectar as a reward; and greenish or violaceous colors. Pollinators were divided into eight functional groups (small bees, syrphids, other dipterans, etc.) and small bees, wasps, and large bees were the most important pollinators. Butterflies, beetles, and hummingbirds were poorly represented, and no bats, hawkmoths, or odor-collecting bees were detected. Plants were grouped in nine pollination systems, among which nectar-flowers pollinated by bees (28%), by wasps or wasps and flies (21%), or by several insect groups (19%) were the most representative. With regard to the degree of specialization, plant species were classified according to their number of pollinator groups. About 33% of the species were monophilous and 30% were oligophilous (i.e., pollinated by one or two functional groups, respectively). The remaining species were either polyphilous (17%) or holophilous (19%), a highly generalist system in which at least three groups act as indistinct pollinators. The general trends of the floral traits and plant-pollinator interactions at the Bocaina grasslands resemble those of biogeographic-connected ecosystems, such as the Venezuelan *arbustal*, and the Brazilian *campo rupestre* and *cerrado*. However, in the Bocaina grasslands, the mean number of pollinator types per plant was 2.09, one of the highest values obtained for worldwide floras. The origin of the high-altitude grasslands is linked to episodes of expansion and retraction due to glacial events. Such a situation may have favored species able to quickly occupy new habitats, including those that do not depend on a few highly specialized pollinators. The prevalence of Asteraceae may also be linked to more generalized pollination systems. Alternatively, some floral traits, such as spontaneous self-pollination and long-lived flowers, may be advantageous for species with more specialized systems in these grasslands with harsh climatic conditions and low rates of pollinator visitation.

Key words: Asteraceae, bees, biogeography, floral biology, generalization, pollination ecology, specialization, syndrome, wasps.

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Plant reproductive processes are believed to help determine the composition and structure of communities (Heithaus, 1974, 1979; Bawa, 1990; Oliveira & Gibbs, 2000). Among such processes, the plant-pollinator interactions form a dynamic, yet somewhat cohesive, ecological subunit of a community, which can be studied in terms of species diversity and distribution, resource utilization, and niche packing, for instance (Moldenke & Lincoln, 1979). In the Neotropics, pollination biology at the community level has been studied in forest areas (Bawa et al., 1985; Kress & Beach, 1994), savanna-like vegetation (Silberbauer-Gottsberger & Gottsberger, 1988; Ramírez, 1989, 2004; Barbosa, 1997; Oliveira & Gibbs, 2000; see also Ramírez & Brito, 1992) and sub-Andean vegetation (Arroyo et al., 1982). In the Brazilian Atlantic Forest Domain, there are several studies on pollination biology in forest areas on both individual species and flower assemblages (Sazima et al., 1995, 1996, 1999; Buzato et al., 2000 and references therein). However, for the high-altitude grasslands or *campos de altitude*—a subtype of the Atlantic Forest Domain—information on plant-pollinator interactions is limited to a few case studies (Martinelli, 1997; Freitas & Sazima, 2001, 2003a, b; Freitas et al., 2006).

The high-altitude grasslands in southeastern Brazil comprise an archipelago of mountaintop formations (ca. 1500 m elevation or higher) along the main mountain ranges, with a North/South orientation. Their origin is connected to glaciation episodes since at least the Late Pleistocene, when these grassland areas are supposed to have experienced periods of expansion and retraction (Ledru et al., 1998). The present high-altitude grasslands have strong biogeographic connections with other high-altitude ecosystems in South America, such as the Andean and Central-American (sub-) alpine habitats, as well as with the Central–Eastern Brazilian rocky and grassy habitats (*campo rupestre*) (Giulietti & Pirani, 1988; Safford, 1999a and references therein). They are also connected to the central Brazilian savannas (*cerrado*) (Silveira & Cure, 1993; see also Modenesi, 1988 for *cerrado* components in palinofloras from the grasslands). These grasslands present—for such restricted areas of habitat—extraordinarily rich floras with many endemics. About one third of the ca. 400 species of the Itatiaia plateau (< 50 km^2), for instance, appear to be endemic to the high-altitude grasslands (Martinelli, 1989). However, many species on the high-altitude grasslands have small populations with few individuals. Owing to such features as high species richness, high endemism, small populations, "island-like" occurrence, biogeographic connections, and harsh climatic conditions for a tropical place, the Brazilian high-altitude grasslands are interesting communities in which to study plant-pollinator interactions.

In pollination biology, the degree of specialization in plant-pollinator relationships has generated a debate in which the traditional view based on the syndrome concept (see Faegri & van der Pijl, 1979) has been counterbalanced by skepticism about the specialized nature of pollination systems (Waser et al., 1996; Herrera, 1996; see also Johnson & Steiner, 2000 and Fenster et al., 2004 for reviews of both views). Surveys of entire local assemblages of plants and their pollinators provide the best evidence to assess the degree of specialization in pollination (Waser et al., 1996), because particular plant-pollinator interactions may be examined on a broad ecological scale, reducing the sampling bias inherent to the comparison of data originating from small scale studies, such as those concerning particular plant taxonomic groups. This paper describes the community-level interactions between plants and pollinators of high-altitude grasslands at the Serra da Bocaina, southeastern Brazil. We studied the floral biology of plant species, recording their sexual systems, flower shapes, dimensions, resources, colors, and pollinators. Combining the data on floral features and functional groups of pollinators allowed us to characterize nine pollination systems in these grasslands and to group plant species in four categories that express the degree of specialization/generalization of plant-pollinator interactions in this community. In addition, we monitored the flowering phenology so as to assess flower resource availability, throughout the year, for the main pollinator groups. We provide a discussion about general patterns of plant-pollinator interactions at the Serra da Bocaina grasslands in relation to other ecosystems with strong biogeographic connections, as well as in relation to the current debate about the prevalence of generalization versus specialization in the plant-pollinator interactions.

Area and Vegetation Studied

The Parque Nacional da Serra da Bocaina (PNSB) —ca. 100,000 hectares—is located between the States of Rio de Janeiro and São Paulo, in southeastern Brazil. Since it extends from sea level to the highest peaks in the Serra da Bocaina (ca. 2100 m), the PNSB shelters many vegetation types of the Brazilian Atlantic Forest Domain. The lower areas are covered mainly by lowland and submontane rainforest, followed by montane and high-altitude forest. Originally, these high-altitude grasslands probably occurred only above 1700–1800 m, but nowadays, due to human disturbance of the forested

areas, they can be found from as low as ca. 1450 m. These grasslands are composed of a matrix of Poaceae and Cyperaceae species mixed with shrubs and herbs from many families, mainly Asteraceae and Melastomataceae. Scattered small trees, mainly species belonging to the genus *Eremanthus* Less. (Asteraceae), can also be found in more protected fields.

In southeastern Brazil, the montane areas encompass two climate regions (Köppen, 1948). Grasslands from the highest summits (above ca. 2000 m) are Cwb, with ≤ 12°C mean annual temperature, cool summers, moderately cold winters with frequent frost, and rare snow. Montane areas at lower elevations can be classified as Cfb (Cwb and Cfb as in Köppen, 1948), i.e., mesothermic, with 12°C–20°C average annual temperature, moderate winters, and mild, wet summers (Segadas-Vianna & Dau, 1965; Nimer, 1977; Safford, 1999a, b). Most grassland areas at Serra da Bocaina are Cfb. Annual precipitation is up to 2100 mm. Rains are concentrated in summer, mainly from December to March. The dry season (Apr. to Sept.) is driest from June to August, with precipitation < 50 mm per month. The effects of seasonal drought on the vegetation are partially offset by thick banks of orographic fog that shroud most Bocaina grasslands, mainly in the early morning, for much of the year. Annual mean temperature is ca. 15°C at 1500–1600 m, and minimum temperatures around 0°C are common during winter (L. Freitas, pers. obs.). During the study period (1998–1999), frosts occurred on more than 30 days per year (L. Freitas, pers. obs.). General information about the vegetation, climate, and topography of southeastern Brazil is available in Segadas-Vianna & Dau (1965), Eiten (1970, 1992), Alonso (1977), Nimer (1977), Moreira & Camelier (1977), and Safford (1999a, b).

Despite its long history in Bocaina highlands, human disturbance was low until the beginning of the 20th century. The primary source of revenue of the inhabitants of this region comes from livestock. Regular fires and grazing are supposed to have negative impacts on the physical environment, the vegetation structure and dynamics, and the welfare of some of the small and endemic plant populations of these grasslands (Safford, 1999a, but see Safford, 2001). Natural fires are apparently rare on these grasslands and are restricted to the wet season, when lightning occurrence is frequent. Anthropogenic fires, however, are frequently set during the dry season, because such an action favors the sprouting of grasses after the rains begin. Some plants may have been eliminated by these regular fires, in particular, species restricted to mesic habitats. However, many of the typical high-altitude taxa, such as the geophytes, have a strong capacity to sprout, apparently as a pre-adaptation against frost, that also seems to be efficient against fires.

This study was carried out in three grassland sites that experienced different fire regimes over the years. Since there is no official register of fire occurrences, information for the last 45–50 years was obtained from both the PNSB staff and the inhabitants of the region. The first area (22°43′57″S, 44°37′06″W) is adjacent to a private farm (Fazenda Mariana) and used to burn every two to three years. The last fire in that area had occurred ca. five months before the beginning of this study (Dec. 1997). The second area (22°44′50″S, 44°36′57″W) is close to Santo Izidro waterfall and used to burn at intervals of five to 10 years. The last fire in this area had occurred five years before the first year of this study, and the area burned again in 1998. Since it presented many treelets and large shrubs, the third area (22°44′12″S, 44°36′55″W) showed marked structural differences. There was no record of fire here when the project started, but the area burned in September 1999.

About 260 plant species belonging to 46 families were recorded during monthly collections in the three study areas and through non-systematic collections in other grassland areas located between 1450 m and 2100 m. Although most families were only represented by a few species, some families, such as Asteraceae (ca. 70 spp.), Poaceae (ca. 35 spp.), Cyperaceae (ca. 15 spp.), Melastomataceae (18 spp.), Orchidaceae, Iridaceae, Rubiaceae, and Solanaceae, were common. Most species were herbs or (sub)shrubs, with small, often lignified and hairy leaves. Many species had leaves with a cupressoid or rosette arrangement, and several perennial plants showed well-developed underground organs (e.g., *Tibouchina minor*, *Microlicia isophylla*, *Esterhazya macrodonta*, *Escallonia farinacea*). Such vegetative features are typical of plants living in high-altitude tropics (Camerik & Werger, 1981; Smith & Young, 1987; Safford, 1999a).

Material and Methods

Between December 1997 and February 2000, we made 25 field trips to Serra da Bocaina, for a total of 211 days of fieldwork. Pollination biology at the community level was studied along a transect ca. 1 km long in each of the three study sites. We studied all plant species located within 5 m of the transects, except Cyperaceae and Poaceae (Table 1). The following floral attributes were noted in the field: shape, symmetry, size, color, and rewards (Table 2). Following Faegri and van der Pijl (1979) and Endress (1994), the flowers were classified into eight different types: inconspicuous, dish (bowl), brush, bell (funnel), flag, gullet, tube, and revolver. Tube types include

Table 1. Plant species, their habit, flowering time, and flowering peak at the Serra da Bocaina grasslands. All collections by the authors are deposited at the UEC, and the collection number (L. Freitas) follows the taxon name in parentheses. Phenological observations occurred from January to December 1999. Species that were found only in the area that burnt in September 1999 are indicated by the symbol (f).

Family/Species	Habit	Flowering time	Flowering peak
Amaryllidaceae			
Hippeastrum glaucescens Mart. (773)	herb	Oct.–Nov.	Nov.
Apiaceae			
Eryngium canaliculatum Cham. & Schltdl. (792)	herb	Nov.–Dec.	Dec.
Eryngium horridum Malme (140)	herb	Jan.–Mar.	Jan.
Apocynaceae			
Gonioanthela hilariana (E. Fourn.) Malme (329)	vine	Mar.–July (f)	Mar.–May
Mandevilla erecta (Vell.) Woodson (86, 509)	sub-shrub	Jan.–Feb.	Jan.
Oxypetalum appendiculatum Mart. (123)	vine	Jan.–Aug. (f)	Apr.–June
Oxypetalum sublanatum Malme (13, 491)	vine	Jan., Mar.–May, Oct. Dec.	Jan., Apr., Nov.–Dec.
Tassadia subulata (Vell.) Fontella & E. A. Schwarz (686)	vine	May–Aug.	June
Aquifoliaceae			
Ilex amara (Vell.) Loes. (656, 797)	sub-shrub	Nov.–Dec.	Nov.–Dec.
Asteraceae			
Achyrocline satureioides (Lam.) DC. (276, 330)	shrub	Jan.–Aug., Dec.	Mar.–June
Baccharis aphylla (Vell.) DC. (707)	sub-shrub	Sep.–Nov.	Sep.–Oct.
Baccharis curitybensis Heering & Dusen (498)	sub-shrub	Jan.–Mar., Dec.	Jan.
Baccharis dracunculifolia DC. (372)	shrub	Mar.–Oct.	Apr.–May, Aug.
Baccharis intermixta Gardner (418)	shrub	May–Aug.	July
Baccharis leptocephala DC. (392, 443, 688)	herb	Apr.–Sep.	May–Aug.
Baccharis pentziifolia Sch. Bip. *ex* Baker (589, 691, 728)	shrub	Jan.–Dec.	Feb., May–Aug., Oct.–Nov.
Baccharis platypoda DC. (334, 863)	shrub	Mar.–June	May
Baccharis tarchonanthoides Baker (733)	sub-shrub	Oct.–Nov.	Oct.–Nov.
Baccharis L. sp. indet. 1 (407)	shrub	July–Aug.	July
Baccharis sp. indet. 2 (441, 689)	shrub	May–July	June–July
Baccharis sp. indet. 3 (108)	shrub	Jan.–Mar.	Jan.
Barrosoa betoniciiformis (DC.) R. M. King & H. Rob. (512, 591)	herb	Jan.–May	Feb.–Mar., May
Campuloclinium megacephalum (Mart. *ex* Baker) R. M. King & H. Rob. (101, 596)	herb	Jan.–May	Feb.–Apr.
Chaptalia integerrima (Vell.) Burkart (744)	herb	Jan.–Feb., Oct.–Dec.	Oct.–Nov.
Chaptalia runcinata var. *graminifolia* (Dusen) Burkart (406, 697)	herb	May–Nov.	July–Aug.
Chromolaena cf. *decumbens* Gardner (100)	herb	Jan.–July	Jan.–Mar.
Chromolaena xylorrhiza (Sch. Bip. *ex* Baker) R. M. King & H. Rob. (835)	herb	Jan.–Feb.	Jan.
Eremanthus erythropappus (DC.) MacLeish (403)	treelet	Jul.–Aug. (f)	Aug.
Erigeron maximus (D. Don) Otto *ex* DC. (64)	shrub	Jan.–Mar., Oct.–Dec.	Jan.–Feb., Dec.
Eupatorium L. sp. indet. 1 (60, 61)	shrub	Jan., Nov.–Dec.	Nov.
Eupatorium sp. indet. 2 (99)	herb	Jan.–July, Dec.	Jan.–Feb.
Eupatorium sp. indet. 3 (326)	herb	Mar.—June	Apr.–May
Eupatorium sp. indet. 4 (374)	herb	Apr.	Apr.
Gochnatia paniculata (Less.) Cabrera (438, 705)	sub-shrub	Aug.–Nov.	Sep.–Oct.
Grazielia gaudichaudeana (DC.) R. M. King & H. Rob. (226, 590)	shrub	Jan.–June	Jan.–Feb.
Hypochaeris gardneri Baker (481)	herb	Jan.–Feb., Oct.–Dec.	Jan.–Feb., Nov.–Dec.
Lucilia lycopodioides (Less.) S. E. Freire (398, 838)	herb	June–Sep.	July–Aug.
Mikania lundiana DC. (393)	vine	May–Jul.	May

Table 1. Continued.

Family/Species	Habit	Flowering time	Flowering peak
Mikania nummularia DC. (440, 690)	shrub	May–Aug.	June–Aug.
Mikania sessilifolia DC. (318, 417, 871)	shrub	Mar.–May	Apr.
Senecio oleosus Vell. (391, 409)	shrub	Jan., Mar.–Sep., Nov.	Mar., July–Aug.
Stevia myriadenia Sch. Bip. *ex* Baker (88, 291)	shrub	Jan.–May	Feb.–Mar.
Symphyopappus compressus (Gardner) B. L. Rob. (57)	shrub	Jan.–Feb. (f)	Jan.
Vernonia herbacea (Vell.) Rusby (741)	herb	Oct.–Dec.	Nov.–Dec.
Vernonia megapotamica Spreng. (36, 536)	herb	Jan.–Apr.	Jan.–Feb.
Vernonia cf. *rosea* Mart. *ex* DC. (275, 592, 844)	sub-shrub	Jan.–Feb.	Feb.
Vernonia tomentella Mart. *ex* DC. (67, 588)	sub-shrub	Jan.–May, Oct.–Dec.	Jan.–Feb., Nov.–Dec.
Vernonia tragiaefolia DC. (626)	sub-shrub	Jan.–Feb., Apr.	Feb.
Vernonia westiniana Less. (92)	shrub	Jan.–June	Feb.
Bromeliaceae			
Dyckia tuberosa (Vell.) Beer (495)	herb	Sep.–Nov.	Oct.–Nov.
Campanulaceae			
Lobelia camporum Pohl (41)	herb	Jan.–June, Nov.–Dec.	Jan.–Feb., June, Dec.
Wahlenbergia brasiliensis Cham. (232, 280)	herb	Jan.–Dec.	Feb., June–Sep.
Clethraceae			
Clethra scabra Pers. var. *scabra* (332)	treelet	Feb.–Aug. (f)	Mar.–May
Convolvulaceae			
Convolvulus crenatifolius Ruiz & Pav. (37, 89)	vine	Jan.–Feb., Dec.	Jan., Dec.
Ipomoea procumbens Mart. (76)	vine	Jan.–Mar.	Feb.
Jacquemontia grandiflora Meisn. (118)	vine	Jan.–Aug., Nov.–Dec.	Jan.–Feb., May–July, Dec.
Cunoniaceae			
Weinmannia organensis Gardner (54, 125)	treelet	Jan.–Aug. (f)	Feb.–Mar., May
Droseraceae			
Drosera montana A. St.-Hil. (127)	herb	Jan.–Feb., Nov.–Dec.	Jan., Dec.
Ericaceae			
Agarista hispidula (DC.) Hook. f. *ex* Nied. (23, 431)	shrub	June–Nov.	Aug.–Sep.
Gaylussacia chamissonis Meisn. (469)	sub-shrub	Apr.–Dec.	Oct.–Dec.
Gaylussacia jordanensis Sleumer (370, 432)	sub-shrub	Jan.–May, Aug.–Dec.	Sep.–Oct.
Eriocaulaceae			
Paepalanthus paulensis Ruhland (706)	herb	Sep.–Dec.	Sep.–Nov.
Paepalanthus polyanthus (Bong.) Kunth (18)	herb	Jan.–June, Nov.–Dec.	Jan.–Apr., Dec.
Erythroxylaceae			
Erythroxylum microphyllum A. St.-Hil. (373, 496)	shrub	Jan.–May, Nov.–Dec.	Jan.–Feb., Dec.
Escalloniaceae			
Escallonia farinacea A. St.-Hil. (507)	shrub	Nov.–Dec.	Nov.
Euphorbiaceae			
Croton dichrous Müll. Arg. (17, 619)	shrub	Jan.–Dec.	Mar.–Jul., Nov.–Dec.
Gentianaceae			
Calolisianthus pedunculatus (Cham. & Schltdl.) Gilg (430, 520)	herb	Jan.–Apr., Dec.	Jan.–Feb.
Calolisianthus pendulus (Mart.) Gilg (80, 264)	herb	Jan.–May, July	Feb.
Deianira nervosa Cham. & Schltdl. (348)	herb	Feb.–Apr., June	Feb.–Mar.
Helia oblongifolia Mart. (1, 95)	herb	Jan.–Mar.	Jan.–Feb.
Zygostigma australe (Cham. & Schltdl.) Griseb. (622)	herb	Feb.–Apr.	Feb.–Mar.
Gesneriaceae			
Sinningia allagophylla (Mart.) Wiehler (9)	herb	Jan.–Mar., Nov.–Dec.	Jan., Dec.

Table 1. Continued.

Family/Species	Habit	Flowering time	Flowering peak
Hypericaceae			
Hypericum brasiliense A. St.-Hil. (218, 508)	shrub	Jan.–May, Dec.	Jan.
Hypericum ternum Choisy (71, 494)	herb	Jan.–Mar., May–Aug., Oct.–Dec.	Jan.–Feb., Nov.–Dec.
Iridaceae			
Alophia geniculata Klatt (376)	herb	Mar.–Apr., Nov.–Dec.	Mar., Nov.
Alophia Herb. sp. indet. 1 (235)	herb	Jan.–Feb.	Jan.
Calydorea campestris (Klatt) Baker (236, 368)	herb	Jan.–Mar., Oct.–Dec.	Jan., Nov.–Dec.
Sisyrinchium micranthum Cav. (762)	herb	Jan.–Feb., Nov.–Dec.	Nov.–Dec.
Sisyrinchium vaginatum Spreng. (346, 434, 515)	herb	Jan., Mar.–Dec.	May–Oct.
Lamiaceae			
Hyptis lippioides Pohl *ex* Benth. (399, 423)	herb	July–Oct.	July
Hyptis plectranthoides Benth. (5, 606)	herb	Jan.–May, Oct.–Dec.	Jan., Dec.
Hyptis umbrosa Salzm. *ex* Benth. (310)	shrub	Jan.–Apr.	Feb.–Mar.
Peltodon radicans Pohl (313, 625)	herb	Mar.–May	Mar.–Apr.
Leguminosae			
Chamaecrista Moench sp. indet. 1 (85)	sub-shrub	Feb.–Mar., Oct.–Dec.	Nov.–Dec.
Crotalaria breviflora DC. (308, 818)	sub-shrub	Jan.–Apr., Dec.	Jan.–Mar.
Lupinus velutinus Benth. (427)	sub-shrub	July–Oct., Dec.	Aug.–Sep.
Lythraceae			
Cuphea glutinosa Cham. & Schltdl. (20)	sub-shrub	Jan.–Dec.	Jan., Apr.–June, Aug., Nov.–Dec.
Malpighiaceae			
Byrsonima variabilis A. Juss. (112, 490)	sub-shrub	Jan.–Feb., May, Oct.–Dec.	Nov.–Dec.
Malvaceae			
Pavonia kleinii Krapov. & Cristóbal (105)	vine	Jan.–Feb., Dec.	Feb.
Sida L. sp. indet. 1 (24, 456)	herb	Jan.–Mar., Oct.–Dec.	Jan., Nov.–Dec.
Melastomataceae			
Leandra erostrata Cogn. (113)	herb	Jan.–Feb., Oct.–Dec.	Jan., Nov.–Dec.
Leandra Raddi sp. indet. 1 (19)	herb	Jan.–Feb., Nov.–Dec.	Jan., Nov.–Dec.
Leandra sp. indet. 2 (401)	shrub	July–Oct.	Aug.–Sep.
Leandra sp. indet. 3 (402)	shrub	July–Dec.	Oct.–Nov.
Microlicia isophylla DC. (103)	sub-shrub	Jan.–Mar., July–Aug., Dec.	Jan.–Feb.
Tibouchina frigidula (DC.) Cogn. (25, 419)	shrub	Jan.–Dec.	Jan.–Mar., Dec.
Tibouchina martialis Cogn. (369)	shrub	Apr.–June	June
Tibouchina minor Cogn. (32)	herb	Jan.–Apr., Dec.	Jan.–Feb.
Trembleya parviflora (D. Don) Cogn. (341, 420)	shrub	Feb.–July	June–July
Trembleya phlogiformis DC. (44, 74)	sub-shrub	Jan.–Mar.	Jan.–Mar.
Ochnaceae			
Ouratea semiserrata (Mart. & Nees) Engl. (425)	treelet	June–July	June
Orchidaceae			
Epidendrum secundum Jacq. (150)	herb	Jan.–Aug. (f)	Jan., Apr.–May
Habenaria parviflora Lindl. (82, 804)	herb	Jan.–Mar., Dec.	Jan.–Feb.
Oncidium barbaceniae Lindl. (282, 305)	herb	Jan.–Mar., May–Dec.	Jan., May, July, Sep.–Dec.
Oncidium blanchetii Rchb. f. (611)	herb	Jan.–Dec.	July–Nov.
Oncidium Sw. sp. indet. 1 (501)	herb	Jan., Dec.	Jan.

Table 1. Continued.

Family/Species	Habit	Flowering time	Flowering peak
Orobanchaceae			
Esterhazya macrodonta Cham. & Schltdl. (244)	shrub	Jan., June–Oct.	July–Aug.
Polygalaceae			
Polygala brasiliensis L. (309, 366, 683)	herb	Feb.–Sep., Nov.–Dec.	Mar., June–Aug., Dec.
Polygala cneorum A. St.-Hil. & Moq. (390)	herb	Apr.–Sep., Nov.	May–Aug.
Rubiaceae			
Borreria capitata (Ruiz & Pav.) DC. (322)	herb	Feb.–July	Mar.–Apr.
Borreria tenella Cham. & Schltdl. (192, 667)	herb	Mar.–July	May–June
Declieuxia cordigera var. *angustifolia* Müll. Arg. (6, 727)	herb	Jan.–Dec.	Jan.–Feb., June, Aug.–Sep.
Galianthe angustifolia (Cham. & Schltdl.) E. L. Cabral (50)	sub-shrub	Jan.–May, July, Sep.–Dec.	Jan.–Feb., Dec.
Galianthe brasiliensis Spreng. (618)	shrub	Jan.–Aug., Oct.–Dec.	Jan.–July, Nov.
Galium hypocarpium (L.) Endl. *ex* Griseb. (371, 802)	sub-shrub	Jan.–July, Oct.–Dec.	Jan., Apr.–May, Nov.–Dec.
Solanaceae			
Solanum aculeatissimum Jacq. (483)	herb	Jan.–Feb., May, Oct.–Dec.	Jan.–Feb., Oct.–Dec.
Solanum americanum Mill. (488, 675)	herb	Jan., Nov.–Dec.	Nov.
Solanum pseudocapsicum L. (768)	sub-shrub	Jan.–Feb., Nov.–Dec.	Jan.–Feb., Nov.
Solanum swartzianum Roem. & Schult. (538, 659)	shrub	Jan., Apr.–June, Aug. (f)	Apr.–May
Solanum viarum Dunal (559, 742)	herb	Jan.–Mar., Aug.–Dec.	Feb., Sep., Nov.–Dec.
Verbenaceae			
Verbena hirta Spreng. (31, 243)	sub-shrub	Jan.–Dec.	Jan., Sep.–Dec.
Violaceae			
Viola cerasifolia A. St.-Hil. (124)	herb	Jan.–Feb., Dec.	Jan., Dec.
Xyridaceae			
Xyris asperula Mart. (846)	herb	Feb.–Mar.	Feb.
Xyris tortulla Mart. (2, 350)	herb	Jan.–May, Dec.	Jan.–Mar.

both salverform and spurred flowers. Asteraceae florets were included in the tube type, and their head as a whole was classified as either dish or brush type. Floral measurements with calipers were performed on at least five fresh flowers, each from different plants. The main flower color was determined using a color guidebook (Kornerup & Wanscher, 1963). For our analysis at the community level, the flowers were grouped into six color sets: i. *violet*—showy combinations of blue and red, such as purple and magenta; ii. *pink*—light colors based on blue or red, such as rose, lavender, and lilac; iii. *red*—orange and red; iv. *yellow*—bright and deep yellow; v. *greenish*—colors with sallow tonalities such as greenish, yellowish, or brownish white; and vi. *white*—bright, apparently pure, white. For many species, pollen fertility was estimated by cytoplasmic stainability, using the acetic carmine test (Radford et al., 1974), and stigmatic receptivity was verified with the H_2O_2 catalase activity test (Zeisler, 1938). In some cases, flowers were tagged and bagged at bud stage, and nectar was extracted on the following day with a graduated microliter syringe (Hamilton, U.S.A.). Nectar volume was registered immediately, and nectar sugar concentration was measured with a hand refractometer (Atago, Japan).

Sexual systems were determined by the presence of both functional anthers and stigmas. Flowers were categorized as either hermaphroditic (monoclinous) or unisexual (diclinous). Plants with unisexual flowers were further classified as monoecious, dioecious, andromonoecious, or gymnomonoecious. Other information about sexual systems—such as the presence of dichogamy and heteromorphy—was noted for some of the species. Spontaneous self-pollination was verified for some species by the report of fruit set in unmanipulated bagged flowers (Kearns & Inouye, 1993). Some pistils were fixed in formaldehyde-

Table 2. Floral features of plant species and their pollination system at the Serra da Bocaina grasslands. In Asteraceae the shape of the blossom (head) and its width are given in parentheses in addition to the tubular florets measurements. Flower size for tube, gullet, bell, and revolver type is effective corolla length vs. opening width; for dish, brush, and inconspicuous type it is the flower width (diameter: d); and for flag type it is keel (k) vs. flag (f) length. Flower symmetry and size for monoecious (U-M) and dioecious (U-D) they plants correspond to female flower first and male flower second, and for gymnomonoecious (GymnM) plants they correspond to hermaphrodite flower first and female flower second. Gynoecium/Androecium = pistil height from the corolla base × stamen height from the corolla base (or spur base in spurred flowers). Flower measurements are the mode.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color[1]	Color group[1]	Floral resource	Pollination system
Amaryllidaceae									
*Hippeastrum glaucescens**	H		tube	Zy, 14 (82) × 7	114 × 96	dark red	RE	N	hummingbird
Apiaceae									
Eryngium canaliculatum	H	protandry	inconsp.	Ac, d1	1 × 1	yellowish green	GR	N, P	uncertain
Eryngium horridum	H	protandry	inconsp.	Ac, d1	2 × 4	yellowish green	GR	N, P	several insect groups
Apocynaceae									
Gonioanthela hilariana	H		dish	Ac, d1	1 × 1	pale yellow	GR	N	wasp/fly
Mandevilla erecta	H	herkogamy	tube	Ac, 13 × 3	5 × 8	pale yellow	GR	N	undet.
Oxypetalum appendiculatum	H		revolver	Ac, 8 × 3	2 × 2	greenish lilac	GR	N	wasp/fly
Oxypetalum sublanatum	H		revolver	Ac, 8 × 5	5 × 5	pale green	GR	N	bee nectar-flower
Tassadia subulata	H		dish	Ac, d1	1 × 1	dark ruby	GR	N	syrphid nectar-flower
Aquifoliaceae									
Ilex amara	U-M	temporal dioecism	bell	Ac, 4 × 2	2 ×	yellowish white	GR	N	bee nectar-flower
				Ac, 4 × 2	× 2			N, P?	
Asteraceae									
Achyrocline satureioides	GymnM	protandry, 2a	tube	Ac, 4 × <1 (14)	5 × 5	light yellow	GR	N	wasp/fly
			(dish)	Ac, 6 × <1	10 ×			N	
Baccharis aphylla	U-D		tube	Ac, 5 × <1 (2)	6 ×	greenish white	GR	N	wasp/fly
			(dish)	Ac, 4 × 1 (5)	× 6			N	
Baccharis curitybensis	U-D		tube	Ac, 5 × <1 (7)	5 ×	pastel yellow	GR	N	wasp/fly
			(dish)	Ac, 5 × <1 (6)	× 6			N	
Baccharis dracunculifolia	U-D		tube	Ac, 2 × <1 (1)	3 ×	yellowish green	GR	N	wasp/fly
			(dish)	Ac, 2 × <1 (4)	× 3			N, P	
Baccharis intermixta	U-D		tube	Ac, 2 × <1 (2)	4 ×	pale yellow	GR	N	wasp/fly
			(dish)	Ac, 3 × <1 (4)	× 4			N	
Baccharis leptocephala	U-D		tube	Ac, 2 × <1 (2)	3 ×	pale yellow	GR	N	wasp/fly
			(dish)	Ac, 3 × <1 (3)	× 4			N	
Baccharis pentziifolia	U-D		tube	Ac, 3 × <1 (2)	5 ×	yellowish green	GR	N	wasp/fly
			(dish)	Ac, 3 × <1 (4)	× 5			N, P	
Baccharis platypoda	U-D		tube	Ac, 3 × <1 (5)	7 ×	grayish yellow	GR	N	wasp/fly

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color[1]	Color group[1]	Floral resource	Pollination system
			(dish)	Ac, 4 × 1 (6)	× 6			N, P	
Baccharis tarchonanthoides	U-D		tube	Ac, 3 × 1 (7)	4 ×	whitish yellow	GR	N	several insect groups
			(dish)	Ac, 2 × 1 (5)	× 3			N	
Baccharis sp. indet. 1	U-D		tube	Ac, 3 × <1 (2)	7 ×	pale yellow	GR	N	wasp/fly
			(dish)	Ac, 4 × <1 (4)	× 7			N	
Baccharis sp. indet. 2	U-D		tube	Ac, 4 × <1 (2)	5 ×	greenish yellow	GR	N	wasp/fly
			(dish)	Ac, 4 × 1 (6)	× 5			N	
Baccharis sp. indet. 3	U-D		tube	Ac, 2 × <1 (1)	4 ×	pale yellow	GR	N	wasp/fly
			(dish)	Ac, 2 × <1 (2)	× 3			N	
Barrosoa betoniciiformis	H	protandry, 2a	tube (brush)	Ac, 3 × <1 (10)	6 × 5	purple	VI	N	several insect groups
Campuloclinium megacephalum	H	protandry, 2a	tube (brush)	Ac, 4 × <1 (16)	9 × 8	reddish purple	VI	N	several insect groups
Chaptalia integerrima	GymnM	protandry, 2a	tube	Ac, 10 × 1 (22)	14 × 3	white	WH	N, P	several insect groups
	Ligulate		(brush)	Zy, 2 × <1	3 ×			N	
Chaptalia runcinata var. *graminifolia*	GymnM	protandry, 2a	tube	Ac, 3 × <1 (12)	4 × 4	yellow	YE	N, P	several insect groups
	Ligulate		(dish)	Zy, 2 × <1	3 ×			N	
Chromolaena cf. *decumbens*	H	protandry, 2a	tube (dish)	Ac, 5 × <1 (9)	7 × 6	reddish violet	VI	N	bee nectar-flower
Chromolaena xylorrhiza	H	protandry, 2a	tube (dish)	Ac, 4 × 1 (4)	6 × 4	purple	VI	N	undet.
Eremanthus erythropappus	H	protandry, 2a	tube (brush)	Ac, 5 × <1 (14)	10 × 8	purple	VI	N, P	several insect groups
Erigeron maximus	GymnM	protandry, 2a	tube	Ac, 4 × 1 (35)	8 × 7	vivid yellow	YE	N, P	several insect groups
	Ligulate		(dish)	Zy, 3 × <1	7 ×			N	
Eupatorium sp. indet. 1	H	protandry, 2a	tube (brush)	Ac, 7 × <1 (10)	15 × 13	white	WH	N, P	bee nectar-flower
Eupatorium sp. indet. 2	H	protandry, 2a	tube (dish)	Ac, 6 × <1 (8)	8 × 7	violet	VI	N	several insect groups
Eupatorium sp. indet. 3	H	protandry, 2a	tube (brush)	Ac, 9 × 1 (12)	19 × 18	purple	VI	N	bee nectar-flower

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color[1]	Color group[1]	Floral resource	Pollination system
Eupatorium sp. indet. 4	H	protandry, 2a	tube (brush)	Ac, 6 × 1 (8)	9 × 8	white	WH	N, P	several insect groups
Gochnatia paniculata	H	protandry, 2a	tube (brush)	Ac, 3 × <1 (10)	8 × 7	greenish yellow	GR	N, P	wasp/fly
Grazielia gaudichaudeana	H	protandry, 2a	tube (brush)	Ac, 3 × <1 (5)	7 × 5	white	WH	N, P	several insect groups
Hypochaeris gardneri	GymnM Ligulate	protandry, 2a	tube (brush)	Ac, 7 × <1 (16) Zy, 5 × <1	10 × 9 11 ×	vivid yellow	YE	N	bee nectar-flower
Lucilia lycopodioides	GymnM Ligulate	protandry, 2a	tube (dish)	Ac, 6 × 1 (3) Zy, 6 × 1	7 × 6 7 ×	yellowish white	GR	N	wasp/fly
Mikania lundiana	H	protandry, 2a	tube (brush)	Ac, 8 × <1 (4)	11 × 9	yellowish white	GR	N, P	bee nectar-flower
Mikania nummularia	H	protandry, 2a	tube (brush)	Ac, 4 × 1 (3)	5 × 4	white	WH	N	wasp/fly
Mikania sessilifolia	H	protandry, 2a	tube (dish)	Ac, 2 × 1 (5)	4 × 3	yellowish white	GR	N	wasp/fly
Senecio oleosus	GymnM Ligulate	protandry, 2a	tube (brush)	Ac, 7 × 1 (40) Zy, 7 × 1	10 × 9 7 ×	vivid yellow	YE	N, P	syrphid/bee nectar-flower
Stevia myriadenia	H	protandry, 2a	tube (brush)	Ac, 5 × <1 (10)	7 × 6	pink	PK	N, P	several insect groups
Symphyopappus compressus	H	protandry, 2a	tube (brush)	Ac, 6 × 1 (7)	12 × 11	white	WH	N, P	several insect groups
Vernonia herbacea	H	protandry, 2a	tube (brush)	Ac, 5 × <1 (15)	11 × 10	purplish magenta	VI	N	bee nectar-flower
Vernonia megapotamica	H	protandry, 2a	tube (brush)	Ac, 2 × 1 (12)	5 × 4	purple	VI	N, P	several insect groups
Vernonia cf. *rosea*	H	protandry, 2a	tube (brush)	Ac, 10 × 1 (21)	15 × 14	purple	VI	N	bee nectar-flower
Vernonia tomentella	H	protandry, 2a	tube (brush)	Ac, 9 × <1 (20)	15 × 14	purple	VI	N, P	bee nectar-flower
Vernonia tragiaefolia	H	protandry, 2a	tube (brush)	Zy, 4 × <1 (9)	9 × 7	magenta	VI	N	bee nectar-flower

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color[1]	Color group[1]	Floral resource	Pollination system
Vernonia westiniana	H	protandry, 2a	tube (brush)	Ac, 6 × <1 (11)	10 × 7	reddish purple	VI	N, P	bee nectar-flower
Bromeliaceae									
Dyckia tuberosa	H	herkogamy	tube	Zy, 13 × 5	10 × 12	reddish orange	RE	N	hummingbird
Campanulaceae									
Lobelia camporum	H	protandry, 2a	gullet	Zy, 8 × 3	14 × 12	lilac	PK	N	bee nectar-flower
Wahlenbergia brasiliensis	H	protandry, 2a	bell	Ac, 3 × 3	5 × 4	lilac	PK	N, P	syrphid/bee nectar-flower
Clethraceae									
Clethra scabra	H		bell	Ac, 2 × 2	2 × 2	yellowish white	GR	N	wasp/fly
Convolvulaceae									
Convolvulus crenatifolius	H	heterandry	bell	Ac, 12 × 14	7 × 7, 6	lavender	PK	N P	syrphid/bee nectar-flower
Ipomoea procumbens	H	herkogamy, heterandry	bell	Ac, 38 × 11	26 × 25, 21	pink	PK	N, P	bee nectar-flower
Jacquemontia grandiflora	H	herkogamy	bell	Ac, 18 × 23	14 × 11	violet	VI	N, P?	bee nectar-flower
Cunoniaceae									
Weinmannia organensis	H		dish	Ac, d3	2 × 2	pale yellow	GR	N	several insect groups
Droseraceae									
Drosera montana	H		dish	Ac, d10	3 × 2	pink	PK	P	syrphid/bee pollen-flower
Ericaceae									
Agarista hispidula	H	2a	tube	Ac, 11 × 2	8 × 7	red	RE	N	hummingbird
Gaylussacia chamissonis	H	2a	bell	Ac, 7 × 3	7 × 5	white	WH	N	bee nectar-flower
Gaylussacia jordanensis	H		bell	Ac, 9 × 6	10 × 5	white	WH	N, P	bee nectar-flower
Eriocaulaceae									
Paepalanthus paulensis	U-M		inconsp.	Ac, d1	2 ×	yellowish white	GR	N	several insect groups
			inconsp.	Ac, d1	× 2			N, P	
Paepalanthus polyanthus	U-M		inconsp.	Ac, d1	2 ×	greenish white	GR	N	several insect groups
			inconsp.	Ac, d1	× 2			N, P	
Erythroxylaceae									
Erythroxylum microphyllum	H	heterostyly	dish	Ac, d7	5 × 2, 2 × 5	pastel yellow	GR	N	wasp/fly

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color[1]	Color group[1]	Floral resource	Pollination system
Escalloniaceae									
Escallonia farinacea	H	protandry, herkogamy	bell	Ac, 3 × 2	5 × 4	white	WH	N	bee nectar-flower
Euphorbiaceae									
Croton dichrous	U-M	temporal dioecism	dish dish	Ac, d2 Ac, d3	2 × × 2	yellowish white	GR	N N, P	wasp/fly
Gentianaceae									
Calolisianthus pedunculatus	H	protandry	tube	Zy, 32 × 12	30 × 29	deep red	RE	N?	undet.
Calolisianthus pendutus	H	protandry, protogyny	tube	Zy, 25 × 9	22 × 20	violet	VI	N?	undet.
Deianira nervosa	H	herkogamy, protogyny	dish	Ac, d15	3 × 2	reddish lilac	PK	P	syrphid/bee pollen-flower
Helia oblongifolia	H	protandry	tube	Zy, 20 × 3	16 × 15	yellowish green	GR	N	undet.
Zygostigma australe	H	protogyny	dish	Ac, d20	3 × 2	purple	VI	P?	syrphid/bee pollen-flower
Gesneriaceae									
Sinningia allagophylla	H	protandry, herkogamy	tube	Zy, 14 × 3	11 × 14	reddish orange	RE	N	hummingbird
Hypericaceae									
Hypericum brasiliense	H	apomixis	dish	Ac, d22	4 × 3	vivid yellow	YE	P	syrphid/bee pollen-flower
Hypericum ternum	H	apomixis	dish	Ac, d22	4 × 3	vivid yellow	YE	P?	uncertain
Iridaceae									
Alophia geniculata	H	herkogamy	bell	Ac, 20 × 14	23 × 12	violet	VI	P, N?	bee pollen-flower
Alophia sp. indet. 1	H	herkogamy	bell	Ac, 20 × 12	10 × 8	lilac	PK	P, N?	uncertain
Calydorea campestris	H		dish	Ac, d28	5 × 4	purplish violet	VI	P	syrphid/bee pollen-flower
Sisyrinchium micranthum	H		tube	Ac, 5 × 2	3 × 3	purple	VI	P, O	syrphid/bee pollen-flower
Sisyrinchium vaginatum	H		dish	Ac, d26	6 × 5	vivid yellow	YE	P, O	syrphid/bee pollen-flower
Lamiaceae									
Hyptis lippioides	H	protandry	gullet	Zy, 4 × 2	12 × 8	grayish violet	VI	N	bee nectar-flower
Hyptis plectranthoides	H	protandry	gullet	Zy, 2 × 1	6 × 5	violet	VI	N	bee nectar-flower

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color[1]	Color group[1]	Floral resource	Pollination system
Hyptis umbrosa	H	protandry	gullet	Zy, 3 × 1	5 × 5	violet	VI	N	bee nectar-flower
Peltodon radicans	H	protandry	gullet	Zy, 5 × 1	8 × 6	bluish violet	VI	N	bee nectar-flower
Leguminosae									
Chamaecrista sp. indet. 1	H	herkogamy, heterandry	bell	Zy, 12 × 7	12 × 12, 4	vivid yellow	YE	P	bee pollen-flower
Crotalaria breviflora	H	heterandry, 2a	flag	Zy, k12 × f12	11 × 10	vivid yellow	YE	N, P	bee nectar-flower
Lupinus velutinus	H	heterandry, 2a	flag	Zy, k13 × f16	12 × 12	violet	VI	P	bee pollen-flower
Lythraceae									
Cuphea glutinosa	H	protandry	tube	Zy, 8 × 2	9 × 9	purple	VI	N	bee nectar-flower
Malpighiaceae									
Byrsonima variabilis	H		dish	Zy, d13 × 10	3 × 3	vivid yellow	YE	O, P	bee oil-flower
Malvaceae									
Pavonia kleinii	H	herkogamy	bell	Ac, 9 × 9	7 × 6	yellow	YE	N, P	bee nectar-flower
Sida sp. indet. 1	H	herkogamy	bell	Ac, 18 × 25	17 × 9	pastel pink	PK	N	bee nectar-flower
Melastomataceae									
Leandra erostrata	H	apomixis?	dish	Ac, d7	6 × 6	pink	PK	P?	uncertain
Leandra sp. indet. 1	H	apomixis?	dish	Ac, d6	5 × 5	white	WH	P?	uncertain
Leandra sp. indet. 2	H	apomixis?	dish	Ac, d7	14 × 12	pink	PK	P?	uncertain
Leandra sp. indet. 3	H	apomixis?	dish	Ac, d8	15 × 13	pink	PK	P?	uncertain
Microlicia isophylla	H	apomixis?, heterandry	dish	Zy, d20	3 × 4	magenta	VI	P	undet.
Tibouchina frigidula	H	heterandry	dish	Zy, d44	14 × 16	deep violet	VI	P	bee pollen-flower
Tibouchina martialis	H	heterandry	dish	Zy, d55	15 × 20	reddish violet	VI	P	bee pollen-flower
Tibouchina minor	H	heterandry	dish	Zy, d30	6 × 7	violet	VI	P	bee pollen-flower
Trembleya parviflora	H	heterandry	dish	Zy, d18	5 × 5	pink	PK	P	bee pollen-flower
Trembleya phlogiformis	H	heterandry	dish	Zy, d22	4 × 4	purple	VI	P	bee pollen-flower
Ochnaceae									
Ouratea semiserrata	H	protandry	dish	Ac, d16	6 × 5	vivid yellow	YE	P	bee pollen-flower
Orchidaceae									
Epidendrum secundum	H		tube	Zy, 5 × <1	6 × 6	purple	VI	N	undet.
Habenaria parviflora	H		tube, spur	Zy, 8 × <1	9 × 9	grayish green	GR	N	undet.
Oncidium barbaceniae	H		dish	Zy, d22 × 19	3 × 2	vivid yellow	YE	O?	uncertain
Oncidium blanchetii	H		dish	Zy, d24 × 15	2 × 2	vivid yellow	YE	O?	undet.
Oncidium sp. indet. 1	H		dish	Zy, d15 × 11	2 × 2	vivid yellow	YE	O?	undet.

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color[1]	Color group[1]	Floral resource	Pollination system
Orobanchaceae									
Esterhazya macrodonta	H	protandry, herkogamy	gullet	Zy, 24 × 10	38 × 34	reddish orange	RE	N	hummingbird
Polygalaceae									
Polygala brasiliensis	H	protandry?	flag	Zy, k2 × f3	2 × 2	reddish purple	VI	N, P?	bee nectar-flower
Polygala cneorum	H	protandry?	flag	Zy, k3 × f4	3 × 3	grayish magenta	VI	N, P?	bee nectar-flower
Rubiaceae									
Borreria capitata	H	herkogamy, protogyny?	tube	Ac, 3 × 1	4 × 4	white	WH	N	several insect groups
Borreria tenella	H	herkogamy, protogyny	tube	Ac, 2 × 1	3 × 3	purple	VI	N	wasp/fly
Declieuxia cordigera var. *angustifolia*	H	heterostyly	tube	Ac, 7 × 1	8 × 6, 6 × 8	purple	VI	N	bee nectar-flower
Galianthe angustifolia	H	heterostyly	tube	Ac, 3 × 1	4 × 2, 2 × 4	yellowish white	GR	N	several insect groups
Galianthe brasiliensis	H	heterostyly	tube	Ac, 3 × 1	4 × 3, 3 × 4	white	WH	N	several insect groups
Galium hypocarpium	H		dish	Ac, d1	2 × 1	greenish yellow	GR	N	wasp/fly
Solanaceae									
Solanum aculeatissimum	AndroM		dish	Ac, d12	10 × 8	vivid yellow	YE	P	bee pollen-flower
Solanum americanum	H		dish	Ac, d4	1 × 1	vivid yellow	YE	P	bee pollen-flower
Solanum pseudocapsicum	H		dish	Ac, d11	4 × 3	vivid yellow	YE	P	bee pollen-flower
Solanum swartzianum	H		dish	Ac, d17	5 × 4	vivid yellow	YE	P	bee pollen-flower
Solanum viarum	AndroM		dish	Ac, d16	10 × 8	yellowish green	GR	P	bee pollen-flower
Verbenaceae									
Verbena hirta	H	herkogamy, heterandry	tube	Ac, 6 × 1	3 × 4, 5	purplish violet	VI	N	bee nectar-flower
Violaceae									
Viola cerasifolia	H	herkogamy	tube	Zy, 6 × 3	6 × 4	violet	VI	P, N	bee pollen-flower
Xyridaceae									
Xyris asperula	H		dish	Ac, d13	4 × 4	vivid yellow	YE	P	syrphid/bee pollen-flower
Xyris tortulla	H	herkogamy	dish	Ac, d22	3 × 3	deep yellow	YE	P	syrphid/bee pollen-flower

Abbreviations: Ac = actinomorphic, AndroM = andromonoecious, D = dioecious, GymnM = gymnomonoecious, H = hermaphrodite, inconsp. = inconspicuous, Ligulate = ligulate floret, M = monoecious, N = nectar, O = oil, P = pollen, U = unisexual (diclinous) flower, undet. = undetermined, Zy = zygomorphic, 2a = secondary pollen presentation.

[1] Main color of corolla, except Solanaceae (anthers) and Cunoniaceae (sepals). Color groups: GR = greenish, PK = pink, RE = red, VI = violet, WH = white, YE = yellow.

* Hummingbirds perch on the corolla of the large *Hippeastrum* flowers (corolla tube length in brackets) during visits. Nectar is concealed in a tube at the corolla base, whose size is the effective corolla length.

alcohol-acetic acid (FAA) at 12 to 60 hours after self or cross hand-pollination and analyzed under fluorescence microscopy to observe pollen tube growth (Martin, 1959). Plants along the transects were checked monthly from December 1998 to February 2000, and two phenology parameters were recorded: flowering time—months in which each species was in flower; and the activity blooming peak—months in which more than 50% of the individuals of each species presented flowers (Table 1).

The pollinators for each species were determined through direct observation of flowers for at least four hours (Tables 3, 4). Observation periods were one to two hours, but longer periods (three to eight hours) were necessary for some species with very low frequency of visits; these were usually observed for a total of 12 or more hours (see Table 4). We concentrated our observations on the most probable time of pollinator visitation for each species. Most observation sessions occurred in the middle of the day, because insects are generally more active in this period. The total observation times only include the observations under good climatic conditions and during the flowering peak of each species. To be considered pollinators, visitors had to have pollen grains attached to their bodies and contact the stigmas during their visits. Hummingbirds were identified in the field or through photographs. Insects visiting the flowers were collected, when possible, with an entomological net. Insect specimens were identified by specialists and deposited at MZSP, ZUEC, and MPEG. Non-captured insect visitors were grouped into different hierarchical categories, at least to order and, in a few cases, to genus level (e.g., *Bombus* Latr.). For the broad community study, we categorized captured and non-captured insect visitors into seven functional groups (after Root, 1967, Cummins, 1973): large bees, small bees, wasps, syrphids, other dipterans, butterflies, and beetles (Tables 4, 5). Large bees are those larger than 12 mm (because it is not indigenous to Brazil, *Apis mellifera* was not included in any bee group).

Plant species were divided into nine pollination systems. For those species that were pollinated by one or two functional groups (monophilous and oligophilous; see below), pollination system was based on sets of floral traits common to plants pollinated by each functional group. A second set of species were pollinated by three or more functional groups of which one or two were clearly identified as main pollinators (polyphilous), and pollination system was designated according to the main pollinator. Main pollinators were defined based on pollinator morphology, behavior, and frequency of visits: usually over 60% or 80% of visits for one or two main groups, respectively; others were designated as secondary pollinators. The final set of species was pollinated by three or more functional groups of apparently similar importance (holophilous) and thus did not have any main pollinator(s). These species were grouped in the pollination system named "several insect groups" (SIG), and their pollinators were designated as indistinct to distinguish them from the secondary and main pollinator categories.

Plant species were classified into four categories representing the degree of specialization/generalization of their interaction with their pollinators: monophily, oligophily, polyphily, and holophily (Table 4). The definition of our first three categories differs from that given by Faegri and van der Pijl (1979), because our unity of reference was functional groups rather than pollinator species. Thus, here, monophily refers to species exclusively pollinated by one functional group. Plant species pollinated by two functional groups (either one or both are their main pollinator[s]) are considered oligophilous. Species pollinated by three or more functional groups are classified either as polyphilous, when one or two groups act as their main pollinators, or holophilous, when there is no preponderance of one or two groups, i.e., when groups act as indistinct pollinators.

Results

We studied a total of 124 species from 35 families (Table 1). Forty species belonged to Asteraceae (32%), followed by Melastomataceae (10 spp., 8%). On the other hand, 16 (46%) and seven (20%) families were represented by only one and two species, respectively.

Floral Biology and Pollinator Agents at the Community Level

A. Floral Traits

The most common flower color groups were violet (29.8% of the 124 species), greenish (28.2%), and yellow (17.0%). Pink (10.5%), white (9.7%), and red (4.8%) were the least represented groups (Table 2). Most flowers were tubular (47.6%) or dish-shaped (28.2%). Since we considered the shape of the head of Asteraceae as a whole instead of each of its florets, dish-shaped blossoms were the most frequent (43.6%), followed by the brush (16.9%), and tube (15.3%) types. Bell (11.3%), and gullet, inconspicuous, flag, and revolver (12.8% altogether) were the least represented flowers (Table 2). Most plants had either actinomorphic (69.4%) or zygomorphic flowers (25.8%), though a small percentage (4.8%) bore both

Table 3. Pollinator species and the plant species it was collected from or observed pollinating (in the case of hummingbirds) at the Serra da Bocaina grasslands. Pollinators that were seen but not collected are included in Table 4. List of the abbreviations of the plant families: AMA, Amaryllidaceae; API, Apiaceae; APO, Apocynaceae; AQU, Aquifoliaceae; AST, Asteraceae; BRO, Bromeliaceae; CAM, Campanulaceae; CLE, Clethraceae; CON, Convolvulaceae; CUN, Cunoniaceae; DRO, Droseraceae; ERIC, Ericaceae; ERIO, Eriocaulaceae; ERY, Erythroxylaceae; ESC, Escalloniaceae; EUP, Euphorbiaceae; GEN, Gentianaceae; GES, Gesneriaceae; HYP, Hypericaceae; IRI, Iridaceae; LAM, Lamiaceae; LEG, Leguminosae; LYT, Lythraceae; MALP, Malpighiaceae; MALV, Malvaceae; MEL, Melastomataceae; OCH, Ochnaceae; ORC, Orchidaceae; ORO, Orobanchaceae; POL, Polygalaceae; RUB, Rubiaceae; SOL, Solanaceae; VER, Verbenaceae; VIO, Violaceae; XYR, Xyridaceae.

Pollinator family and species	Plant family	Plant species
Trochiliformes		
Trochilidae (hummingbirds)		
Chlorostilbon aureoventris berlepschi Pinto	ERIC:	*Agarista hispidula*
Clytolaema rubricauda (Boddaert)	GES:	*Sinningia allagophylla*
Colibri serrirostris (Vieillot)	BRO:	*Dyckia tuberosa*
	GES:	*Sinningia allagophylla*
Leucochloris albicollis (Vieillot)	AMA:	*Hippeastrum glaucescens*
	ERIC:	*Agarista hispidula*
	GES:	*Sinningia allagophylla*
	ORO:	*Esterhazya macrodonta*
Stephanoxis lalandi lalandi (Vieillot)	GES:	*Sinningia allagophylla*
Coleoptera (beetles)		
Buprestidae (jewel beetles)		
Conognatha Cobos sp. indet. 1	ERIO:	*Paepalanthus paulensis*
Cantharidae (soldier beetles)		
Discodon tucumanum Pic	ERIO:	*Paepalanthus paulensis*
Cantharidae sp. indet. 1	API:	*Eryngium canaliculatum*
	AST:	*Baccharis pentziifolia*, *Baccharis tarchonanthoides*, *Barrosoa betoniciiformis*, *Campuloclinium megacephalum*, *Chaptalia integerrima*, *Erigeron maximus*, *Eupatorium* sp. indet. 2, *Grazielia gaudichaudeana*
	ERIO:	*Paepalanthus polyanthus*
Cantharidae sp. indet. 2	CLE:	*Clethra scabra*
	CUN:	*Weinmannia organensis*
Cerambicidae (longhorn beetles)		
Rhinotragus festivus Perty	CLE:	*Clethra scabra*
Elateridae (click beetles)		
Cardiorhinus Eschscholtz sp. indet. 1	API:	*Eryngium canaliculatum*
Melyridae (softwinged flower beetles)		
Astylus sexmaculatus Perty	AST:	*Eupatorium* sp. indet. 4
Diptera (flies)		
Bombyliidae (beeflies)		
Euprepina Hull sp. indet. 1	AST:	*Campuloclinium megacephalum*
Exoprosopa Macquart sp. indet. 1	RUB:	*Borreria capitata*
Paravilla Painter sp. indet. 1	AST:	*Campuloclinium megacephalum*, *Chaptalia runcinata*, *Stevia myriadenia*, *Vernonia megapotamica*
Culicidae (biting flies)		
Culicidae sp. indet. 1	API:	*Eryngium horridum*
Curtonotidae (curtonotid flies)		
Curtonotidae sp. indet. 1	API:	*Eryngium horridum*
	AST:	*Baccharis platypoda*, *Mikania sessilifolia*
Curtonotidae sp. indet. 2	RUB:	*Galianthe angustifolia*
Sarcophagidae (flesh flies)		
Sarcophagidae sp. indet. 1	RUB:	*Galianthe angustifolia*
Sarcophagidae sp. indet. 2	ERIO:	*Paepalanthus paulensis*

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
Sciaridae (sciarid flies)		
Sciaridae sp. indet. 1	AST:	*Baccharis aphylla, Baccharis tarchonanthoides*
	ERIO:	*Paepalanthus paulensis*
Syrphidae (hover-flies)		
Allograpta exotica (Wiedemann)	CAM:	*Wahlenbergia brasiliensis*
	GEN:	*Zygostigma australe*
	IRI:	*Alophia* sp. indet. 1, *Sisyrinchium micranthum*
	RUB:	*Galianthe angustifolia*
Palpada rufipedes Thompson	APO:	*Tassadia subulata*
Pseudodoros clavatus (Fabricius)	RUB:	*Borreria capitata, Galianthe brasiliensis*
Syrphus phaeostigma Wiedemann	AST:	*Baccharis leptocephala*
Toxomerus watsoni (Curran)	APO:	*Tassadia subulata*
	AST:	*Achyrocline satureioides, Baccharis leptocephala, Baccharis pentziifolia, Baccharis tarchonanthoides, Chaptalia runcinata, Gochnatia paniculata, Mikania sessilifolia, Senecio oleosus*
	CAM:	*Wahlenbergia brasiliensis*
	DRO:	*Drosera montana*
	ERIO:	*Paepalanthus paulensis, Paepalanthus polyanthus*
	EUP:	*Croton dichrous*
	IRI:	*Alophia geniculata, Sisyrinchium vaginatum*
	LYT:	*Cuphea glutinosa*
	RUB:	*Borreria capitata, Galianthe brasiliensis*
	XYR:	*Xyris asperula, Xyris tortulla*
Toxomerus Macquart sp. indet. 1	APO:	*Tassadia subulata*
	AST:	*Achyrocline satureioides, Chaptalia runcinata*
	ERIO:	*Paepalanthus paulensis*
	IRI:	*Sisyrinchium vaginatum*
	RUB:	*Borreria capitata*
Syrphidae sp. indet. 1	DRO:	*Drosera montana*
	XYR:	*Xyris asperula*
Syrphidae sp. indet. 2	IRI:	*Alophia geniculata*
Syrphidae sp. indet. 3	AST:	*Baccharis pentziifolia*
Syrphidae sp. indet. 4	XYR:	*Xyris tortulla*
Syrphidae sp. indet. 5	AST:	*Mikania sessilifolia, Stevia myriadenia*
	GEN:	*Deianira nervosa*
	IRI:	*Calydorea campestris*
Syrphidae sp. indet. 6	AST:	*Chaptalia runcinata*
Tachinidae (tachinid flies)		
Cylindromyia dorsalis (Wiedemann)	AST:	*Grazielia gaudichaudeana*
	HYP:	*Hypericum brasiliense*
Jurinella cf. *corpulenta* (Townsend)	API:	*Eryngium horridum*
	AST:	*Baccharis dracunculifolia, Baccharis platypoda, Mikania sessilifolia*
Tachinidae sp. indet. 1	AST:	*Eupatorium* sp. indet. 2
	RUB:	*Galianthe brasiliensis*
Tachinidae sp. indet. 2	CLE:	*Clethra scabra*
Tachinidae sp. indet. 3	ERIO:	*Paepalanthus paulensis*
Tachinidae sp. indet. 4	AST:	*Baccharis* sp. indet. 2
	RUB:	*Galianthe brasiliensis*
Tachinidae sp. indet. 5	AST:	*Eremanthus erythropappus*
Tachinidae sp. indet. 6	AST:	*Vernonia westiniana*
Tachinidae sp. indet. 7	RUB:	*Galianthe angustifolia*
Tachinidae sp. indet. 8	AST:	*Achyrocline satureioides, Baccharis dracunculifolia, Symphyopappus compressus*
Tachinidae sp. indet. 9	API:	*Eryngium horridum*
Tephritidae (fruit flies)		
Trupanea Schrank sp. indet. 1	RUB:	*Galium hypocarpium*

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
Family indet. (flies)		
Diptera sp. indet. 1	API:	*Eryngium horridum*
Diptera sp. indet. 2	AST:	*Chaptalia runcinata*
Diptera sp. indet. 3	AST:	*Chaptalia runcinata*
Diptera sp. indet. 4	AST:	*Baccharis dracunculifolia*
Diptera sp. indet. 5	ERIO:	*Paepalanthus polyanthus*
Diptera sp. indet. 6	AST:	*Erigeron maximus*
Diptera sp. indet. 7	CLE:	*Clethra scabra*
Diptera sp. indet. 8	ERIO:	*Paepalanthus polyanthus*
Hymenoptera		
Andrenidae, Panurginae (dagger bees)		
Anthrenoides Ducke sp. indet. 1	VIO:	*Viola cerasifolia*
Apidae, Apini (honey bees)		
Apis mellifera Linnaeus	AQU:	*Ilex amara*
	AST:	*Baccharis dracunculifolia, Baccharis pentziifolia, Baccharis platypoda, Baccharis* sp. indet. 2, *Barrosoa betoniciiformis, Campuloclinium megacephalum, Eremanthus erythropappus, Eupatorium* sp. indet. 2, *Grazielia gaudichaudeana, Hypochaeris gardneri, Mikania lundiana, Stevia myriadenia, Symphyopappus compressus, Vernonia westiniana*
	CAM:	*Wahlenbergia brasiliensis*
	CLE:	*Clethra scabra*
	CON:	*Convolvulus crenatifolius*
	ERIC:	*Gaylussacia chamissonis, Gaylussacia jordanensis*
	EUP:	*Croton dichrous*
	IRI:	*Sisyrinchium vaginatum*
	LAM:	*Hyptis lippioides, Hyptis plectranthoides, Hyptis umbrosa, Peltodon radicans*
	LYT:	*Cuphea glutinosa*
	RUB:	*Borreria capitata, Galianthe angustifolia, Galianthe brasiliensis*
	VER:	*Verbena hirta*
Apidae, Bombini (bumblebees)		
Bombus atratus Franklin	APO:	*Oxypetalum sublanatum*
	AST:	*Campuloclinium megacephalum, Chromolaena* cf. *decumbens, Stevia myriadenia, Symphyopappus compressus, Vernonia tomentella, Vernonia westiniana*
	CAM:	*Lobelia camporum*
	CON:	*Ipomoea procumbens, Jacquemontia grandiflora*
	IRI:	*Alophia geniculata*
	LAM:	*Hyptis lippioides, Hyptis plectranthoides*
	LEG:	*Crotalaria breviflora, Lupinus velutinus*
	LYT:	*Cuphea glutinosa*
	MEL:	*Tibouchina frigidula, Tibouchina minor, Trembleya phlogiformis*
	RUB:	*Declieuxia cordigera, Galianthe angustifolia*
	VER:	*Verbena hirta*
Bombus brasiliensis Lepeletier	AST:	*Stevia myriadenia, Vernonia westiniana*
	LEG:	*Crotalaria breviflora*
	LYT:	*Cuphea glutinosa*
	VER:	*Verbena hirta*
Bombus morio (Swederus)	AST:	*Vernonia westiniana*
	LYT:	*Cuphea glutinosa*
	RUB:	*Galianthe angustifolia*
	VER:	*Verbena hirta*
Apidae, Centridini (digger bees)		
Centris burgdorfi Friese	CAM:	*Lobelia camporum*
	RUB:	*Declieuxia cordigera*

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
Centris discolor Smith	MALP:	*Byrsonima variabilis*
	MEL:	*Tibouchina frigidula*
Centris cf. *insularis* Smith	MALP:	*Byrsonima variabilis*
Centris klugi Friese	AST:	*Hypochaeris gardneri, Vernonia* cf. *rosea, Vernonia tomentella*
	LEG:	*Chaemaecrista* sp. indet. 1
	LYT:	*Cuphea glutinosa*
	MALP:	*Byrsonima variabilis*
	MEL:	*Tibouchina minor*
Centris tarsata Smith	MALP:	*Byrsonima variabilis*
	VER:	*Verbena hirta*
Centris (Melacentris) Moure sp. indet. 1	MALP:	*Byrsonima variabilis*
Apidae, Ceratinini (dwarf carpenter bees)		
Ceratina cf. *asuncionis* Strand	AST:	*Senecio oleosus, Vernonia herbacea, Vernonia tomentella*
	CAM:	*Lobelia camporum*
	MALV:	*Sida* sp. indet. 1
	VER:	*Verbena hirta*
Ceratina Latreille sp. indet. 1	LYT:	*Cuphea glutinosa*
Ceratina sp. indet. 2	CON:	*Convolvulus crenatifolius*
Apidae, Ericrocidini		
Mesonychium caerulescens Lepeletier & Serville	AST:	*Vernonia tomentella*
	LYT:	*Cuphea glutinosa*
	RUB:	*Galianthe angustifolia*
	VER:	*Verbena hirta*
Apidae, Eucerini (long-horned bees)		
Gaesischia nigra Moure	AST:	*Vernonia tragiaefolia*
Melissoptila aureocincta Urban	AST:	*Symphyopappus compressus*
Apidae, Meliponini (stingless bees)		
Melipona bicolor bicolor Lepeletier	AST:	*Eremanthus erythropappus, Eupatorium* sp. indet. 3, *Grazielia gaudichaudeana, Mikania lundiana, Vernonia megapotamica, Vernonia tomentella, Vernonia westiniana*
	CLE:	*Clethra scabra*
	ERIC:	*Gaylussacia chamissonis*
	IRI:	*Alophia geniculata*
	LAM:	*Hyptis lippioides*
	MEL:	*Trembleya parviflora*
	OCH:	*Ouratea semiserrata*
Melipona quadrifasciata anthidioides (Lepeletier)	AST:	*Campuloclinium megacephalum, Eremanthus erythropappus, Mikania lundiana, Symphyopappus compressus*
Paratrigona subnuda Moure	AST:	*Chaptalia integerrima, Eremanthus erythropappus, Mikania lundiana*
Plebeia droryana (Friese)	AST:	*Achyrocline satureioides*
Plebeia saiqui (Friese)	API:	*Eryngium horridum*
	AQU:	*Ilex amara*
	AST:	*Vernonia westiniana*
	ERI:	*Gaylussacia jordanensis*
	IRI:	*Alophia geniculata, Calydorea campestris*
	LAM:	*Hyptis lippioides*
	MALP:	*Byrsonima variabilis*
Scaptotrigona bipunctata (Lepeletier)	CLE:	*Clethra scabra*
Schwarziana quadripunctata (Lepeletier)	AST:	*Baccharis* sp. indet. 2, *Eremanthus erythropappus, Eupatorium* sp. indet. 4, *Grazielia gaudichaudeana, Mikania lundiana*
	CLE:	*Clethra scabra*
	HYP:	*Hypericum brasiliense*

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
Trigona spinipes (Fabricius)	AST:	*Baccharis* sp. indet. 2
	ERIO:	*Paepalanthus paulensis*
	LAM:	*Hyptis lippioides*
Apidae, Tapinotaspidini (digger bees)		
Monoeca Lepeletier & Serville sp. indet. 1	MALP:	*Byrsonima variabilis*
Paratetrapedia (Lophopedia) cf. *pygmaea* (Schrottky)	AST:	*Stevia myriadenia*
	XYR:	*Xyris tortulla*
Paratetrapedia (Xanthopedia) Michener & Moure sp. indet. 1	MALP:	*Byrsonima variabilis*
Paratetrapedia (Trigonopedia) Moure sp. indet. 1	AST:	*Stevia myriadenia*
Apidae, Xylocopini (giant carpenter bees)		
Xylocopa brasilianorum (Linnaeus)	AST:	*Symphyopappus compressus*
	CON:	*Ipomoea procumbens*
	MEL:	*Tibouchina frigidula, Tibouchina martialis*
	VER:	*Verbena hirta*
Braconidae (braconid wasps)		
Braconidae sp. indet. 1	AST:	*Baccharis platypoda*
Chrysididae (cuckoo wasps)		
Chrysididae sp. indet. 1	AST:	*Baccharis dracunculifolia*
Colletidae, Colletini (plasterer bees)		
Colletes Latreille sp. indet. 1	AST:	*Hypochaeris gardneri*
	ESC:	*Escallonia farinacea*
Eurytomidae (eurytomid wasps)		
Eurytomidae sp. indet. 1	RUB:	*Galium hypocarpium*
Gasteruptiidae (gasteruptid wasps)		
Gasteruptiinae sp. indet. 1	EUP:	*Croton dichrous*
Halictidae, Augochlorini (sweat bees)		
Augochlorodes turrifaciens Moure	VIO:	*Viola cerasifolia*
Augochloropsis cf. *cognata* Moure	AQU:	*Ilex amara*
	AST:	*Campuloclinium megacephalum, Vernonia tomentella*
	CLE:	*Clethra scabra*
	EUP:	*Croton dichrous*
	IRI:	*Calydorea campestris*
	LAM:	*Hyptis lippioides*
	MALP:	*Byrsonima variabilis*
	MALV:	*Pavonia kleinii*
	RUB:	*Borreria capitata, Galianthe brasiliensis*
Augochloropsis cyanea (Schrottky)	AST:	*Barrosoa betoniciiformis, Campuloclinium megacephalum, Chaptalia runcinata, Eupatorium* sp. indet. 4, *Grazielia gaudichaudeana, Vernonia tomentella*
	ERIC:	*Gaylussacia jordanensis*
	EUP:	*Croton dichrous*
	LYT:	*Cuphea glutinosa*
	RUB:	*Galianthe angustifolia, Galianthe brasiliensis*
	SOL:	*Solanum aculeatissimum, Solanum pseudocapsicum, Solanum swartzianum, Solanum viarum*
	XYR:	*Xyris asperula*
Augochloropsis iris (Schrottky)	AST:	*Campuloclinium megacephalum*
	IRI:	*Alophia geniculata*
Augochloropsis Cockerell sp. indet. 1	AST:	*Eupatorium* sp. indet. 2, *Stevia myriadenia*

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
	ERIC:	*Gaylussacia chamissonis*, *Gaylussacia jordanensis*
	LAM:	*Hyptis umbrosa*
	LYT:	*Cuphea glutinosa*
	MEL:	*Trembleya phlogiformis*
	POL:	*Polygala cneorum*
	RUB:	*Galianthe brasiliensis*
	SOL:	*Solanum pseudocapsicum*
Ceratalictus Moure sp. indet. 1	AQU:	*Ilex amara*
	AST:	*Vernonia westiniana*
	ERIC:	*Gaylussacia jordanensis*
	ERY:	*Erythroxylum microphyllum*
	GEN:	*Zygostigma australe*
	IRI:	*Alophia* sp. indet. 1
	LAM:	*Hyptis lippioides*, *Hyptis plectranthoides*, *Hyptis umbrosa*
	RUB:	*Borreria capitata*, *Borreria tenella*, *Galianthe brasiliensis*
Paroxystoglossa cf. *jocasta* (Schrottky)	IRI:	*Alophia geniculata*
Paroxystoglossa Moure sp. indet. 1	AST:	*Chaptalia integerrima*
Pseudaugochlora cf. *graminea* (Fabricius)	VER:	*Verbena hirta*
Augochlorini sp. indet. 1	RUB:	*Declieuxia cordigera*
Halictidae, Halictini (sweat bees)		
Agapostemon Guerin-Meneville sp. indet. 1	AST:	*Symphyopappus compressus*
Dialictus Robertson sp. indet. 1	ERIC:	*Gaylussacia jordanensis*
	IRI:	*Alophia geniculata*, *Calydorea campestris*, *Sisyrinchium micranthum*
	OCH:	*Ouratea semiserrata*
	VIO:	*Viola cerasifolia*
Dialictus sp. indet. 2	AST:	*Chaptalia runcinata*
Pseudagapostemon cyaneus Moure & Sakagami	AST:	*Mikania lundiana*, *Senecio oleosus*
Halictini sp. indet. 1	HYP:	*Hypericum brasiliense*
Halictini sp. indet. 2	IRI:	*Alophia geniculata*
	VER:	*Verbena hirta*
Leucospidae (leucospid wasps)		
Leucospidae sp. indet. 1	AST:	*Baccharis intermixta*
Megachilidae, Anthidiini (mason and carder bees)		
Anthidium sertanicola Moure & Urban	LEG:	*Crotalaria breviflora*
	LYT:	*Cuphea glutinosa*
Epanthidium autumnale (Schrottky)	AST:	*Stevia myriadenia*
Megachilidae, Megachilini (leaf-cutter, mason and cuckoo bees)		
Coelioxys Latreille sp. indet. 1	AST:	*Erigeron maximus*, *Senecio oleosus*
Coelioxys sp. indet. 2	AST:	*Stevia myriadenia*
Megachile cf. *anthidioides* Radoskowski	AST:	*Symphyopappus compressus*
	LYT:	*Cuphea glutinosa*
Megachile iheringi Schrottky	AST:	*Eupatorium* sp. indet. 1, *Vernonia tomentella*
	ERIC:	*Gaylussacia jordanensis*
	HYP:	*Hypericum brasiliense*
	LEG:	*Lupinus velutinus*
Megachile laeta Smith	LEG:	*Lupinus velutinus*
	VER:	*Verbena hirta*

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
Megachile terrestris Schrottky	AST:	*Eupatorium* sp. indet. 1, *Vernonia tomentella*
Pompilidae (spider wasps)		
Pompilidae sp. indet. 1	AST:	*Baccharis* sp. indet. 2
Pompilidae sp. indet. 2	AST:	*Baccharis platypoda*
Pompilidae sp. indet. 3	AST:	*Baccharis* sp. indet. 2
Pompilidae sp. indet. 4	AST:	*Baccharis* sp. indet. 2
Scoliidae (digger wasps)		
Scoliidae sp. indet. 1	AST:	*Symphyopappus compressus*, *Vernonia westiniana*
Sphecidae (mud-dauber and sphecid wasps)		
Bicyrtes paranae Bohart	RUB:	*Galianthe angustifolia*
Pryonyx thomaz (Fabricius)	AST:	*Baccharis dracunculifolia*
Sphex dorsalis Lepeletier	RUB:	*Galianthe angustifolia*
Sphex opacus Dahlbom	AST:	*Eupatorium* sp. indet. 4
Cercerini sp. indet. 1	CLE:	*Clethra scabra*
Cercerini sp. indet. 2	AST:	*Mikania nummularia*
	CLE:	*Clethra scabra*
Larrinae sp. indet. 1	AST:	*Achyrocline satureioides*
Tenthredinidae (sawflies)		
Tenthredinidae sp. indet. 1	RUB:	*Galianthe brasiliensis*
Tiphiidae (tiphiid wasps)		
Tiphiidae sp. indet. 1	AST:	*Baccharis* sp. indet. 2
Vespidae (paper wasps)		
Agelaia vicina (Saussure)	AST:	*Baccharis intermixta*
	ERIO:	*Paepalanthus polyanthus*
Brachygastra lecheguana (Latreille)	AST:	*Baccharis* sp. indet. 3
Mischocyttarus drewseni Saussure	AQU:	*Ilex amara*
	AST:	*Achyrocline satureioides*, *Baccharis aphylla*, *Baccharis dracunculifolia*, *Baccharis pentziifolia*, *Baccharis* sp. indet. 2, *Chaptalia integerrima*, *Eupatorium* sp. indet. 4, *Gochnatia paniculata*
	CLE:	*Clethra scabra*
	ERY:	*Erythroxylum microphyllum*
	EUP:	*Croton dichrous*
	RUB:	*Galianthe brasiliensis*
Polistes billardieri Fabricius	AQU:	*Ilex amara*
	AST:	*Achyrocline satureioides*, *Baccharis* sp. indet. 2, *Baccharis* sp. indet. 3, *Gochnatia paniculata*, *Mikania sessilifolia*
	ERY:	*Erythroxylum microphyllum*
	RUB:	*Galianthe brasiliensis*
Polistes cinerascens Saussure	APO:	*Gonioanthela hilariana*
	AST:	*Baccharis dracunculifolia*, *Baccharis platypoda*
Polybia fastidiosuscula Saussure	AST:	*Baccharis platypoda*, *Baccharis* sp. indet. 2
	CLE:	*Clethra scabra*
	RUB:	*Galianthe angustifolia*
Polybia minarum Ducke	CLE:	*Clethra scabra*
	CUN:	*Weinmannia organensis*
Polybia scutellaris (White)	AST:	*Baccharis tarchonanthoides*
	EUP:	*Croton dichrous*
Polybia sericea (Olivier)	APO:	*Gonioanthela hilariana*, *Oxypetalum appendiculatum*
	RUB:	*Borreria tenella*
Protonectarina sylveirae (Saussure)	AST:	*Baccharis curitybensis*
Protopolybia sedula (Saussure)	AST:	*Baccharis* sp. indet. 2
Synoeca cyanea (Fabricius)	CLE:	*Clethra scabra*
Family indet. (wasps)		
Hymenoptera sp. indet. 1	AST:	*Achyrocline satureioides*, *Mikania nummularia*
Hymenoptera sp. indet. 2	AST:	*Lucilia lycopodioides*, *Mikania nummularia*

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
	ERY:	*Erythroxylum microphyllum*
	RUB:	*Borreria capitata, Borreria tenella*
Hymenoptera sp. indet. 3	AST:	*Mikania sessilifolia*
	LYT:	*Cuphea glutinosa*
Hymenoptera sp. indet. 4	AST:	*Baccharis aphylla*
Hymenoptera sp. indet. 5	AST:	*Baccharis pentziifolia*
Hymenoptera sp. indet. 6	AST:	*Eupatorium* sp. indet. 2
Hymenoptera sp. indet. 7	AST:	*Achyrocline satureioides*
Hymenoptera sp. indet. 8	AST:	*Achyrocline satureioides*
Hymenoptera sp. indet. 9	AST:	*Achyrocline satureioides*
Hymenoptera sp. indet. 10	AST:	*Baccharis pentziifolia*
	CLE:	*Clethra scabra*
Hymenoptera sp. indet. 11	LYT:	*Cuphea glutinosa*
Hymenoptera sp. indet. 12	RUB:	*Galianthe brasiliensis*
Hymenoptera sp. indet. 13	AST:	*Grazielia gaudichaudeana*
Hymenoptera sp. indet. 14	AST:	*Baccharis dracunculifolia*
Hymenoptera sp. indet. 15	RUB:	*Galianthe angustifolia*
Lepidoptera (butterflies)		
Hesperiidae (skippers and darters)		
Sarbia cf. *damippe* (Mabille & Boullet)	AST:	*Barrosoa betoniciiformis, Campuloclinium megacephalum*
Sarbia cf. *xanthippe* (Latreille)	AST:	*Vernonia westiniana*
Thespieus Godman sp. indet. 1	AST:	*Campuloclinium megacephalum*
Urbanus Hübner sp. indet. 1	VER:	*Verbena hirta*
Hesperiinae sp. indet. 1	AST:	*Grazielia gaudichaudeana*
Pyrrhopyginae sp. indet. 1	AST:	*Chaptalia integerrima, Vernonia westiniana*
Lycaenidae (coppers and hair streaks)		
Thecla Fabricius sp. indet. 1	AST:	*Chaptalia runcinata, Mikania nummularia, Vernonia westiniana*
	RUB:	*Galianthe brasiliensis*
Riodininae sp. indet. 1	API:	*Eryngium horridum*
Nymphalidae (danaids and browns)		
Agraulis vanillae maculosa (Stichel)	AST:	*Vernonia megapotamica*
Vanessa myrinna (Doubleday)	AST:	*Campuloclinium megacephalum, Eupatorium* sp. indet. 1, *Eupatorium* sp. indet. 4, *Vernonia tomentella*
Vanessa Fabricius sp. indet. 1	AST:	*Eupatorium* sp. indet. 3
Yphthimoides ochracea (Butler)	AST:	*Symphyopappus compressus*
	CLE:	*Clethra scabra*
Pieridae (whites and yellows)		
Eurema nise tenella (Boisduval)	LYT:	*Cuphea glutinosa*
	VER:	*Verbena hirta*
Hesperocharis erota (Lucas)	AST:	*Vernonia westiniana*

types. Small flowers were predominant. Out of the 65 species with tubular or gullet flowers, for instance, 55.4% had corolla tubes ≤ 5 mm long, whereas only 13.8% had tubes >10 mm long. Nectar was the exclusive or main resource of 71.0% of the species. Although pollinators fed on or collected pollen from more than half of the species, it was the exclusive resource of only 17.7% of the species. Even though we only measured the nectar production of a few species, low nectar production (i.e., less than 2 μl) prevailed.

The great majority of species presented hermaphroditic flowers (82.3%), and a few were either monoecious (3.2%) or dioecious (8.9%) (Table 2). The latter group only comprised the 11 species of *Baccharis* Mill. (Asteraceae). Seven other species of Asteraceae (5.6%) presented both hermaphroditic and unisexual (ligulate) flowers (gymnomonoecism). We detected spontaneous self-pollination in some species including plants that were also pollinated by animals (Table 4).

Table 4. Plant species, time of observation, pollination system, degree of specialization/generalization, and collected and observed pollinators at the Serra da Bocaina grasslands. Abbreviations: N = nocturnal observation; undet. = undetermined pollination system; MONO = monophily, OLIGO = oligophily, POLI = polyphily, HOLO = holophily, n/a = not applicable; BL = large bees, BS = small bees, CO = beetles, DI = flies except syrphids, HB = hummingbirds, LE = butterflies, SSP = spontaneous self-pollination, SY = syrphids, WA = wasps; ? = information to be confirmed; uncoll = uncollected insect pollinators (only observed).

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Amaryllidaceae				
Hippeastrum glaucescens	18.5	hummingbird	MONO	HB - *Leucochloris albicollis*
Apiaceae				
Eryngium canaliculatum	4	uncertain	n/a	CO - *Cardiorhinus* sp. indet. 1, Cantharidae sp. indet. 1.
Eryngium horridum	4	several insect groups	HOLO	BS - *Plebeia saiqui*; DI - *Jurinella* cf. *corpulenta*, Culicidae sp. indet. 1, Curtonotidae sp. indet. 1, Tachinidae sp. indet. 9, Diptera sp. indet. 1; LE - Riodininae sp. indet. 1; SY - uncoll (1 sp.); WA - uncoll (1 sp.)
Apocynaceae				
Gonioanthela hilariana	5.5	wasp/fly	MONO	WA - *Polistes cinerascens*, *Polybia sericea*
Mandevilla erecta	18 N	undet.	n/a	not visited
Oxypetalum appendiculatum	7.5	wasp/fly	MONO	WA - *Polybia sericea*
Oxypetalum sublanatum	11	bee nectar-flower	MONO	BL - *Bombus atratus*
Tassadia subulata	15	syrphid nectar-flower	MONO	SY - *Palpada rufipedes*, *Toxomerus watsoni*, *Toxomerus* sp. indet. 1, uncoll (1 sp.)
Aquifoliaceae				
Ilex amara	4.5	bee nectar-flower	OLIGO	*Apis mellifera*; BS - *Augochloropsis* cf. *cognata*, *Ceratalictus* sp. indet. 1, *Plebeia saiqui*; WA - *Mischocyttarus drewseni*, *Polistes billardieri*, uncoll Vespidae (1 sp.), Pompilidae (1 sp.)
Asteraceae				
Achyrocline satureioides	6	wasp/fly	POLI	BS - *Plebeia droryana*; DI - Tachinidae sp. indet. 8; SY - *Toxomerus watsoni*, *Toxomerus* sp. indet. 1, uncoll (2 spp.); WA - *Mischocyttarus drewseni*, *Polistes billardieri*, Larrinae sp. indet. 1, Hymenoptera sp. indet. 1, Hymenoptera sp. indet. 7, Hymenoptera sp. indet. 8, Hymenoptera sp. indet. 9, uncoll (1 sp.)
Baccharis aphylla	7	wasp/fly	OLIGO	DI - Sciaridae sp. indet. 1; WA - *Mischocyttarus drewseni*, Hymenoptera sp. indet. 4, uncoll (1 sp.)
Baccharis curitybensis	4	wasp/fly	MONO	WA - *Protonectarina sylveirae*

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Baccharis dracunculifolia	7.5	wasp/fly	OLIGO	*Apis mellifera*; DI - *Jurinella* cf. *corpulenta*, Tachinidae sp. indet. 8, Diptera sp. indet. 4; WA - *Mischocyttarus drewseni*, *Polistes cinerascens*, *Pryonyx thomaz*, Chrysididae sp. indet. 1, Hymenoptera sp. indet. 14
Baccharis intermixta	4	wasp/fly	MONO	WA - *Agelaia vicina*, Leucospidae sp. indet. 1, uncoll (1 sp.)
Baccharis leptocephala	4	wasp/fly	OLIGO	SY - *Syrphus phaeostigma*, *Toxomerus watsoni*; WA - uncoll (2 spp.)
Baccharis pentziifolia	9.5	wasp/fly	POLI	*Apis mellifera*; CO - Cantharidae sp. indet. 1; DI - uncoll (1 sp.); SY - *Toxomerus watsoni*, Syrphidae sp. indet. 3; WA - *Mischocyttarus drewseni*, Hymenoptera sp. indet. 5, Hymenoptera sp. indet. 10, uncoll (1 sp.)
Baccharis platypoda	4	wasp/fly	POLI	*Apis mellifera*; BS - uncoll Augochlorini (1 sp.); DI - *Jurinella* cf. *corpulenta*, Curtonotidae sp. indet. 1; WA - *Polistes cinerascens*, *Polybia fastidiosuscula*, Braconidae sp. indet. 1, Pompilidae sp. indet. 2.
Baccharis tarchonanthoides	4	several insect groups	HOLO	BS - uncoll Augochlorini (1 sp.); CO - Cantharidae sp. indet. 1; DI - Sciaridae sp. indet. 1, uncoll Tachinidae (2 spp.); SY - *Toxomerus watsoni*, uncoll (1 sp.); WA - *Polybia scutellaris*
Baccharis sp. indet. 1	4	wasp/fly	MONO	WA - uncoll (1 sp.)
Baccharis sp. indet. 2	7	wasp/fly	POLI	*Apis mellifera*; BS - *Schwarziana quadripunctata*, *Trigona spinipes*; DI - Tachinidae sp. indet. 4; WA - *Mischocyttarus drewseni*, *Polistes billardieri*, *Polybia fastidiosuscula*, *Protopolybia sedula*, Pompilidae sp. indet. 1, Pompilidae sp. indet. 3, Pompilidae sp. indet. 4, Tiphiidae sp. indet. 1, uncoll Vespidae (2 spp.)
Baccharis sp. indet. 3	4	wasp/fly	MONO	WA - *Brachygastra lecheguana*, *Polistes billardieri*
Barrosoa betoniciiformis	4	several insect groups	HOLO	*Apis mellifera*; BS - *Augochloropsis cyanea*; CO - Cantharidae sp. indet. 1; LE - *Sarbia* cf. *damippe*, uncoll (1 sp.)
Campuloclinium megacephalum	11.5	several insect groups	HOLO	*Apis mellifera*; BS - *Melipona quadrifasciata*, *Augochloropsis cyanea*, *A. iris*, *A.* cf. *cognata*, uncoll Augochlorini (1 sp.); BL - *Bombus atratus*; CO - Cantharidae sp. indet. 1; DI - *Euprepina* sp. indet. 1, *Paravilla* sp. indet. 1, uncoll Bombyliidae (2 sp.); LE - *Sarbia* cf. *damippe*, *Thespeius* sp. indet. 1, *Vanessa myrinna*, uncoll *Vanessa* (1 sp.), Hesperiidae (1 sp.) uncoll (1 sp.); WA - uncoll Pompilidae (1 sp.), Sphecidae (1 sp.)

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Chaptalia integerrima	5	several insect groups	HOLO	BS - *Paratrigona subnuda*, *Paroxystoglossa* sp. indet. 1, uncoll Halictidae (2 spp.); CO - Cantharidae sp. indet. 1; LE - Pyrrhopyginae sp. indet. 1, uncoll Lycaenidae (1 sp.); WA - *Mischocyttarus drewseni*, uncoll Eunemidae (1 sp.), Vespidae (1 sp.)
Chaptalia runcinata var. *graminifolia*	13.5	several insect groups	HOLO	BS - *Augochloropsis cyanea*, *Dialictus* sp. indet. 2; DI - *Paravilla* sp. indet. 1, Diptera sp. indet. 2, Diptera sp. indet. 3, uncoll Bombyliidae (1 sp.); LE - *Thecla* sp. indet. 1, uncoll Hesperiidae (1 sp.); SY - *Toxomerus watsoni*, *Toxomerus* sp. indet. 1, Syrphidae sp. indet. 6
Chromolaena cf. *decumbens*	7.5	bee nectar-flower	MONO	BL - *Bombus atratus*
Chromolaena xylorrhiza	4	undet.	n/a	not visited
Eremanthus erythropappus	5	several insect groups	HOLO	*Apis mellifera*; BS - *Melipona bicolor*, *M. quadrifasciata*, *Paratrigona subnuda*, *Schwarziana quadripunctata*; BL - uncoll *Bombus* (1 sp.); DI - Tachinidae sp. indet. 5; LE - uncoll Hesperiidae (1 sp.), *Vanessa* (2 spp.); SY - uncoll (1 sp.); WA - uncoll Pompilidae (1 sp.), Sphecidae (1 sp.)
Erigeron maximus	4	several insect groups	HOLO	BS - *Coelioxys* sp. indet. 1, uncoll Augochlorini (1 sp.); CO - Cantharidae sp. indet. 1; DI -Diptera sp. indet. 6
Eupatorium sp. indet. 1	6	bee nectar-flower	OLIGO	BL - *Megachile iheringi*, *M. terrestris*; LE - *Vanessa myrinna*, uncoll Lycaenidae (1 sp.)
Eupatorium sp. indet. 2	9.5	several insect groups	HOLO	*Apis mellifera*; BS - *Augochloropsis* sp. indet. 1; BL - uncoll *Bombus* (1 sp.); CO - Cantharidae sp. indet. 1; DI - Tachinidae sp. indet. 1; LE - uncoll Hesperiidae (2 spp.); WA - Hymenoptera sp. indet. 6, uncoll (1 sp.)
Eupatorium sp. indet. 3	4	bee nectar-flower	OLIGO	BS - *Melipona bicolor*; LE - *Vanessa* sp. indet. 1
Eupatorium sp. indet. 4	6	several insect groups	HOLO	BS - *Schwarziana quadripunctata*, *Augochloropsis cyanea*; CO - *Astylus sexmaculatus*; DI - uncoll Bombyliidae (1 sp.), Tachinidae (1 sp.); LE - *Vanessa myrinna*; SY - uncoll (1 sp.); WA - *Mischocyttarus drewseni*, *Sphex opacus*
Gochnatia paniculata	4	wasp/fly	OLIGO	SY - *Toxomerus watsoni*, uncoll (2 sp.); WA - *Mischocyttarus drewseni*, *Polistes billardieri*, uncoll Pompilidae (1 sp.), Vespidae (2 spp.)

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Grazielia gaudichaudeana	5	several insect groups	HOLO	*Apis mellifera*; BS - *Melipona bicolor*, *Schwarziana quadripunctata*, *Augochloropsis cyanea*; CO - Cantharidae sp. indet. 1, uncoll (1 sp.); DI - *Cylindromyia dorsalis*; LE - Hesperiinae sp. indet. 1; WA - Hymenoptera sp. indet. 13, uncoll (1 sp.)
Hypochaeris gardneri	5.5	bee nectar-flower	OLIGO	*Apis mellifera*; BS - *Colletes* sp. indet. 1; BL - *Centris klugi*
Lucilia lycopodioides	12.5	wasp/fly	MONO	WA - Hymenoptera sp. indet. 2, uncoll Vespidae (3 spp.)
Mikania lundiana	4.5	bee nectar-flower	POLI	*Apis mellifera*; BS - *Melipona bicolor*, *M. quadrifasciata*, *Paratrigona subnuda*, *Schwarziana quadripunctata*, *Pseudagapostemon cyaneus*; LE - uncoll *Vanessa* (1 sp.); WA - uncoll Pompilidae (1 sp.)
Mikania nummularia	7	wasp/fly	OLIGO	LE - *Thecla* sp. indet. 1, uncoll Hesperiidae (1 sp.); WA - Cercerini sp. indet. 2, Hymenoptera sp. indet. 1, Hymenoptera sp. indet. 2
Mikania sessilifolia	6.5	wasp/fly	POLI	DI - *Jurinella* cf. *corpulenta*, Curtonotidae sp. indet. 1, uncoll Curtonotidae (1 sp.), Tachinidae (3 spp.); SY - *Toxomerus watsoni*, Syrphidae sp. indet. 5; WA - *Polistes billardieri*, Hymenoptera sp. indet. 3, uncoll Vespidae (2 spp.)
Senecio oleosus	5	syrphid/bee nectar-flower	POLI	BS - *Ceratina* cf. *asuncionis*, *Pseudagapostemon cyaneus*, *Coelioxys* sp. indet. 1, uncoll Halictini (1 sp.); BL - uncoll *Bombus* (1 sp.); SY - *Toxomerus watsoni*, uncoll (2 spp.)
Stevia myriadenia	23	several insect groups	HOLO	*Apis mellifera*; BS - *Paratetrapedia (Lophopedia)* cf. *pygmaea*, *P. (Trigonopedia)* sp. indet. 1, *Augochloropsis* sp. indet. 1, *Epanthidium autumnale*, *Coelioxys* sp. indet. 2, uncoll Augochlorini (1 sp.); BL - *Bombus atratus*, *B. brasiliensis*, uncoll *Centris* (1 sp.); DI - *Paravilla* sp. indet. 1, uncoll Bombyliidae (1 sp.); SY - Syrphidae sp. indet. 5, uncoll (1 sp.)
Symphyopappus compressus	5	several insect groups	HOLO	*Apis mellifera*; BS - *Melipona quadrifasciata*, *Melissoptila aureocincta*, *Agapostemon* sp. indet. 1, *Megachile* cf. *anthidioides*; BL - *Bombus atratus*, *Xylocopa brasilianorum*; DI - Tachinidae sp. indet. 8; LE - *Yphthimoides ochracea*, uncoll Nymphalidae (2 sp.), Pieridae (1 sp.); WA - Scoliidae sp. indet. 1, uncoll (1 sp.)
Vernonia herbacea	8.5	bee nectar-flower	OLIGO	BS - *Ceratina* cf. *asuncionis*; BL - uncoll *Bombus*

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Vernonia megapotamica	12	several insect groups	HOLO	BS - *Melipona bicolor*, uncoll Meliponini (2 spp.), Halictidae (3 spp.); DI - *Paravilla* sp. indet. 1; LE - *Agraulis vanillae*; WA - uncoll Pompilidae (1 sp.), Vespidae (2 spp.)
Vernonia cf. *rosea*	4	bee nectar-flower	MONO	BL - *Centris klugi*, uncoll *Bombus*
Vernonia tomentella	8	bee nectar-flower	POLI	BS - *Melipona bicolor*, *Mesonychium caerulescens*, *Ceratina* cf. *asuncionis*, *Augochloropsis* cf. *cognata*, *A. cyanea*, uncoll Halictini (1 sp.); BL - *Bombus atratus*, *Centris klugi*, *Megachile iheringi*, *M. terrestris*, uncoll *Bombus*; LE - *Vanessa myrinna*
Vernonia tragiaefolia	4	bee nectar-flower	OLIGO	BS - *Gaesischia nigra*; BL - uncoll *Bombus*
Vernonia westiniana	8	bee nectar-flower	POLI	*Apis mellifera*; BS - *Melipona bicolor*, *Plebeia saiqui*, *Ceratalictus* sp. indet. 1, uncoll Meliponini (1 sp.), Halictidae (2 spp.); BL - *Bombus atratus*, *B. brasiliensis*, *B. morio*, uncoll *Centris* (2 spp.); DI - Tachinidae sp. indet. 6, uncoll Tachinidae (2 spp.); LE - *Sarbia* cf. *xanthippe*, Pyrrhopyginae sp. indet. 1, *Thecla* sp. indet. 1, *Hesperocharis erota*, uncoll Hesperiidae (1 sp.), Nymphalidae (5 spp.), Pieridae (1 sp.), Sphingidae (1 sp.); WA - Scoliidae sp. indet. 1, uncoll Pompilidae (1 sp.), Vespidae (1 sp.)
Bromeliaceae				
Dyckia tuberosa	10	hummingbird	MONO	HB - *Colibri serrirostris*
Campanulaceae				
Lobelia camporum	7	bee nectar-flower	OLIGO	BS - *Ceratina* cf. *asuncionis*; BL - *Bombus atratus*, *Centris burgdorfi*, uncoll *Bombus*
Wahlenbergia brasiliensis	15	syrphid/bee nectar-flower	OLIGO	*Apis mellifera*; BS - uncoll Augochlorini (2 spp.); SY - *Allograpta exotica*, *Toxomerus watsoni*, uncoll (2 spp.)
Clethraceae				
Clethra scabra	7.5	wasp/fly	POLI	*Apis mellifera*; BS - *Melipona bicolor*, *Scaptotrigona bipunctata*, *Schwarziana quadripunctata*, *Augochloropsis* cf. *cognata*, uncoll Meliponini (2 spp.), Halictidae (3 spp.); CO - Cantharidae sp. indet. 2, *Rhinotragus festivus*; DI - Tachinidae sp. indet. 2, Diptera sp. indet. 7, uncoll Sarcophagidae (1 sp.), Tachinidae (1 sp.); LE - *Yphthimoides ochracea*; WA - *Mischocyttarus drewseni*, *Synoeca cyanea*, *Polybia fastidiosuscula*, *P. minarum*, Cercerini sp. indet. 1, Cercerini sp. indet. 2, Hymenoptera sp. indet. 10, uncoll (1 sp.)

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Convolvulaceae				
Convolvulus crenatifolius	4	syrphid/bee nectar-flower	OLIGO	*Apis mellifera*; BS - *Ceratina* sp. indet. 2, uncoll *Ceratina* (1 sp.); SY - uncoll (1 sp.)
Ipomoea procumbens	6	bee nectar-flower	MONO	BL - *Bombus atratus*, *Xylocopa brasilianorum*, uncoll *Bombus*
Jacquemontia grandiflora	9	bee nectar-flower	POLI	BS - uncoll Meliponini (1 sp.), Tapinotaspidini (1 sp.), Halictidae (3 spp.); BL - *Bombus atratus*, uncoll *Bombus*, *Centris* (1 sp.); WA - uncoll Vespidae (1 sp.)
Cunoniaceae				
Weinmannia organensis	8	several insect groups	HOLO	CO - Cantharidae sp. indet. 2; LE - uncoll (1 sp.); WA - *Polybia minarum*
Droseraceae				
Drosera montana	6	syrphid/bee pollen-flower	MONO	SY - *Toxomerus watsoni*, Syrphidae sp. indet. 1, uncoll (1 sp.)
Ericaceae				
Agarista hispidula	38.5	hummingbird, SSP	MONO	HB - *Chlorostilbon aureoventris*, *Leucochloris albicollis*
Gaylussacia chamissonis	16.5	bee nectar-flower	OLIGO	*Apis mellifera*; BS - *Melipona bicolor*, *Augochloropsis* sp. indet. 1, uncoll Meliponini (1 sp.); WA - uncoll *Polybia* (2 spp.)
Gaylussacia jordanensis	31.5	bee nectar-flower	POLI	*Apis mellifera*; BS - *Plebeia saiqui*, *Augochloropsis cyanea*, *Augochloropsis* sp. indet. 1, *Ceratalictus* sp. indet. 1, *Dialictus* sp. indet. 1, uncoll Meliponini (1 sp.), Halictidae (1 sp.); BL - *Megachile iheringi*; WA - uncoll Vespidae (1 sp.)
Eriocaulaceae				
Paepalanthus paulensis	8	several insect groups	HOLO	BS - *Trigona spinipes*; CO - *Conognatha* sp. indet. 1, *Discodon tucumanum*; DI - Sarcophagidae sp. indet. 2, Sciaridae sp. indet. 1, Tachinidae sp. indet. 3, uncoll (1 sp.); LE - uncoll Hesperiidae (1 sp.); SY - *Toxomerus watsoni*, *Toxomerus* sp. indet. 1, uncoll (3 spp.); WA - uncoll Vespidae (1 sp.)
Paepalanthus polyanthus	4	several insect groups	HOLO	CO - Cantharidae sp. indet. 1; DI – Diptera sp. indet. 5, Diptera sp. indet. 8, uncoll Bombyliidae (1 sp.); LE - uncoll (1 sp.); SY - *Toxomerus watsoni*; WA - *Agelaia vicina*
Erythroxylaceae				
Erythroxylum microphyllum	6	wasp/fly	OLIGO	BS - *Ceratalictus* sp. indet. 1, uncoll Meliponini (1 sp.), Augochlorini (2 spp.); WA - *Mischocyttarus drewseni*, *Polistes billardieri*, Hymenoptera sp. indet. 2, uncoll Pompilidae (1 sp.), Vespidae (2 spp.)

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Escalloniaceae				
Escallonia farinacea	6	bee nectar-flower	MONO	BS - *Colletes* sp. indet. 1
Euphorbiaceae				
Croton dichrous	6	wasp/fly	POLI	*Apis mellifera*; BS - *Augochloropsis* cf. *cognata*, *A. cyanea*; DI - uncoll Tachinidae (2 spp.); SY - *Toxomerus watsoni*; WA - *Mischocyttarus drewseni*, *Polybia scutellaris*, Gasteruptiinae sp. indet. 1, uncoll Vespidae (2 spp.)
Gentianaceae				
Calolisianthus pedunculatus	19.5	undet., SSP	n/a	not visited
Calolisianthus pendulus	38.5	undet., SSP	n/a	not visited
Deianira nervosa	6	syrphid/bee pollen-flower, SSP	MONO	SY - Syrphidae sp. indet. 5
Helia oblongifolia	20 N	undet., SSP	n/a	not visited
Zygostigma australe	8.5	syrphid/bee pollen-flower, SSP	OLIGO	BS - *Ceratalictus* sp. indet. 1; SY - *Allograpta exotica*, uncoll (1 sp.)
Gesneriaceae				
Sinningia allagophylla	27	hummingbird	MONO	HB - *Clytolaema rubricauda*, *Colibri serrirostris*, *Leucochloris albicollis*, *Stephanoxis lalandi*
Hypericaceae				
Hypericum brasiliense	8	syrphid/bee pollen-flower, apomictic	POLI	BS - *Schwarziana quadripunctata*, Halictini sp. indet. 1; BL - *Megachile iheringi*; DI - *Cylindromyia dorsalis*; SY - uncoll (1 sp.)
Hypericum ternum	-	uncertain, apomictic	n/a	n/a
Iridaceae				
Alophia geniculata	11	bee pollen-flower	POLI	BS - *Melipona bicolor*, *Plebeia saiqui*, *Augochloropsis iris*, *Paroxystoglossa* cf. *jocasta*, *Dialictus* sp. indet. 1, Halictini sp. indet. 2, uncoll Tapinotaspidini (1 sp.); BL - *Bombus atratus*; SY - *Toxomerus watsoni*, Syrphidae sp. indet. 2
Alophia sp. indet. 1	7	uncertain	n/a	BS - *Ceratalictus* sp. indet. 1; SY - *Allograpta exotica*
Calydorea campestris	8.5	syrphid/bee pollen-flower	OLIGO	BS - *Plebeia saiqui*, *Augochloropsis* cf. *cognata*, *Dialictus* sp. indet. 1; SY - Syrphidae sp. indet. 5, uncoll (2 spp.)
Sisyrinchium micranthum	5	syrphid/bee pollen-flower	OLIGO	BS - *Dialictus* sp. indet. 1; SY - *Allograpta exotica*

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Sisyrinchium vaginatum	21.5	syrphid/bee pollen-flower	OLIGO	*Apis mellifera*; BS - uncoll Augochlorini (2 spp.); SY - *Toxomerus watsoni*, *Toxomerus* sp. indet. 1, uncoll (1 sp.)
Lamiaceae				
Hyptis lippioides	7	bee nectar-flower	OLIGO	*Apis mellifera*; BS - *Melipona bicolor*, *Plebeia saiqui*, *Trigona spinipes*, *Augochloropsis* cf. *cognata*, *Ceratalictus* sp. indet. 1; BL - *Bombus atratus*
Hyptis plectranthoides	6.5	bee nectar-flower	OLIGO	*Apis mellifera*; BS - *Ceratalictus* sp. indet. 1; BL - *Bombus atratus*, uncoll *Bombus*
Hyptis umbrosa	4	bee nectar-flower	OLIGO	*Apis mellifera*; BS - *Augochloropsis* sp. indet. 1, *Ceratalictus* sp. indet. 1; WA - uncoll Vespidae (2 spp.)
Peltodon radicans	4	bee nectar-flower	MONO	*Apis mellifera*
Leguminosae				
Chamaecrista sp. indet. 1	6	bee pollen-flower	MONO	BL - *Centris klugi*
Crotalaria breviflora	7	bee nectar-flower	OLIGO	BS - *Anthidium sertanicola*; BL - *Bombus atratus*, *B. brasiliensis*
Lupinus velutinus	27	bee pollen-flower, SSP	MONO	BL - *Megachile iheringi*, *M. laeta*, *Bombus atratus*, uncoll *Bombus*, *Megachile* (1 spp.)
Lythraceae				
Cuphea glutinosa	24	bee nectar-flower	POLI	*Apis mellifera*; BS - *Ceratina* sp. indet. 1, *Mesonychium caerulescens*, *Augochloropsis cyanea*, *Augochloropsis* sp. indet. 1, *Anthidium sertanicola*, *Megachile* cf. *anthidioides*; BL - *Bombus atratus*, *B. brasiliensis*, *B. morio*, *Centris klugi*; LE - *Eurema nise tenella*; SY - *Toxomerus watsoni*; WA - Hymenoptera sp. indet. 3, Hymenoptera sp. indet. 11
Malpighiaceae				
Byrsonima variabilis	16	bee oil-flower	OLIGO	BS - *Plebeia saiqui*, *Augochloropsis* cf. *cognata*, *Monoeca* sp. indet. 1, *Paratetrapedia (Xanthopedia)* sp. indet. 1, *Centris* cf. *insularis*; BL - *Centris discolor*, *C. klugi*, *C. tarsata*, *Centris (Melacentris)* sp. indet. 1, uncoll *Centris* (2 spp.)
Malvaceae				
Pavonia kleinii	4	bee nectar-flower	MONO	BS - *Augochloropsis* cf. *cognata*
Sida sp. indet. 1	6	bee nectar-flower	MONO	BS - *Ceratina* cf. *asuncionis*, uncoll *Ceratina* (1 sp.)
Melastomataceae				
Leandra erostrata	5	uncertain, apomictic?	n/a	not visited

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Leandra sp. indet. 1	6	uncertain, apomictic?	n/a	not visited
Leandra sp. indet. 2	11	uncertain, apomictic?	n/a	not visited
Leandra sp. indet. 3	6.5	uncertain, apomictic?	n/a	not visited
Microlicia isophylla	14.5	uncertain, apomictic?	n/a	not visited
Tibouchina frigidula	24	bee pollen-flower	MONO	BL - *Bombus atratus*, *Xylocopa brasilianorum*, *Centris discolor*, uncoll *Bombus*, *Centris* (2 spp.)
Tibouchina martialis	4	bee pollen-flower	MONO	BL - *Xylocopa brasilianorum*, uncoll *Centris* (1 sp.)
Tibouchina minor	10	bee pollen-flower	OLIGO	BS - uncoll Augochlorini (1 sp.); BL - *Bombus atratus*, *Centris klugi*, uncoll *Centris* (2 spp.)
Trembleya parviflora	6	bee pollen-flower	MONO	BS - *Melipona bicolor*
Trembleya phlogiformis	7	bee pollen-flower	OLIGO	BS - *Augochloropsis* sp. indet. 1; BL - *Bombus atratus*
Ochnaceae				
Ouratea semiserrata	7	bee pollen-flower	OLIGO	BS - *Melipona bicolor*, *Dialictus* sp. indet. 1; BL - uncoll *Centris* (1 sp.)
Orchidaceae				
Epidendrum secundum	14	undet.	n/a	not visited
Habenaria parviflora	5, 13 N	undet.	n/a	not visited
Oncidium barbaceniae	19.5	uncertain	n/a	uncoll *Bombus*
Oncidium blanchetii	14	undet.	n/a	not visited
Oncidium sp. indet. 1	14	undet.	n/a	not visited
Orobanchaceae				
Esterhazya macrodonta	72.5	hummingbird	MONO	HB - *Leucochloris albicollis*
Polygalaceae				
Polygala brasiliensis	6.5	bee nectar-flower, SSP?	MONO	BS - uncoll Augochlorini (1 sp.)
Polygala cneorum	10	bee nectar-flower, SSP?	MONO	BS - *Augochloropsis* sp. indet. 1

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Rubiaceae				
Borreria capitata	8.5	several insect groups	HOLO	*Apis mellifera*; BS - *Augochloropsis* cf. *cognata*, *Ceratalictus* sp. indet. 1; DI - *Exoprosopa* sp. indet. 1, uncoll Sarcophagidae (1 sp.); SY - *Pseudodoros clavatus*, *Toxomerus watsoni*, *Toxomerus* sp. indet. 1, uncoll (1 sp.); WA - Hymenoptera sp. indet. 2, uncoll Vespidae (1 sp.)
Borreria tenella	5	wasp/fly	OLIGO	BS - *Ceratalictus* sp. indet. 1; WA - *Polybia sericea*, Hymenoptera sp. indet. 2, uncoll Vespidae (2 spp.)
Declieuxia cordigera var. *angustifolia*	7	bee nectar-flower	POLI	BS - Augochlorini sp. indet. 1, uncoll Augochlorini (1 sp.); BL - *Bombus atratus*, *Centris burgdorfi*, uncoll *Bombus*; LE - uncoll Hesperiidae (1 sp.); WA - uncoll Vespidae (1 sp.)
Galianthe angustifolia	24	several insect groups	HOLO	*Apis mellifera*; BS - *Mesonychium caerulescens*, *Augochloropsis cyanea*, uncoll Augochlorini (2 spp.); BL - *Bombus atratus*, *B. morio*, uncoll *Centris* (2 spp.); DI - Curtonotidae sp. indet. 2, Sarcophagidae sp. indet. 1, Tachinidae sp. indet. 7; LE - uncoll Hesperiidae (1 sp.); SY - *Allograpta exotica*, uncoll (2 spp.); WA - *Bicyrtes paranae*, *Sphex dorsalis*, *Polybia fastidiosuscula*, Hymenoptera sp. indet. 15, uncoll Vespidae (2 spp.)
Galianthe brasiliensis	8	several insect groups	HOLO	*Apis mellifera*; BS - *Augochloropsis* cf. *cognata*, *Augochloropsis cyanea*, *Augochloropsis* sp. indet. 1, *Ceratalictus* sp. indet. 1; DI - Tachinidae sp. indet. 1, Tachinidae sp. indet. 4; LE - *Thecla* sp. indet. 1; SY - *Pseudodoros clavatus*, *Toxomerus watsoni*, uncoll (1 sp.); WA - *Mischocyttarus drewseni*, *Polistes billardieri*, Tenthredinidae sp. indet. 1, Hymenoptera sp. indet. 12, uncoll Pompilidae (1 sp.), Sphecidae (1 sp.), Vespidae (3 spp.)
Galium hypocarpium	11.5	wasp/fly	OLIGO	DI - *Trupanea* sp. indet. 1, WA - Eurytomidae sp. indet. 1
Solanaceae				
Solanum aculeatissimum	9.5	bee pollen-flower	MONO	BS - *Augochloropsis cyanea*
Solanum americanum	8.5	bee pollen-flower	MONO	BS - uncoll Augochlorini (1 sp.)
Solanum pseudocapsicum	5.5	bee pollen-flower	MONO	BS - *Augochloropsis cyanea*, *Augochloropsis* sp. indet. 1
Solanum swartzianum	4.5	bee pollen-flower	MONO	BS - *Augochloropsis cyanea*
Solanum viarum	13	bee pollen-flower	MONO	BS - *Augochloropsis cyanea*

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Verbenaceae				
Verbena hirta	10	bee nectar-flower	POLI	*Apis mellifera*; BS - *Mesonychium caerulescens*, *Ceratina* cf. *asuncionis*, *Pseudaugochlora* cf. *graminea*, Halictini sp. indet. 2; BL - *Bombus atratus*, *B. brasiliensis*, *B. morio*, *Xylocopa brasilianorum*, *Centris tarsata*, *Megachile laeta*; LE - *Urbanus* sp. indet. 1, *Eurema nise*, uncoll *Vanessa* (1 sp.); SY - uncoll (2 spp.); WA - uncoll Vespidae (1 sp.)
Violaceae				
Viola cerasifolia	27	bee pollen-flower	MONO	BS - *Anthrenoides* sp. indet. 1, *Augochlorodes turrifaciens*, *Dialictus* sp. indet. 1
Xyridaceae				
Xyris asperula	4	syrphid/bee pollen-flower	OLIGO	BS - *Augochloropsis cyanea*, uncoll Meliponini (1 sp.), Augochlorini (1 sp.); SY - *Toxomerus watsoni*, Syrphidae sp. indet. 1, uncoll (2 spp.)
Xyris tortulla	6	syrphid/bee pollen-flower	OLIGO	BS - *Paratetrapedia* cf. *pygmaea*; SY - *Toxomerus watsoni*, Syrphidae sp. indet. 4, uncoll (2 spp.)

Table 5. Number of plant species exclusively, mainly, and secondarily pollinated by each pollinator group at the Serra da Bocaina grasslands. Percentages are given in parentheses (n = 106 plant species). Because many species are pollinated by two to six pollinator groups the sum of the totals exceeds 100%.

	Role in pollination			
Pollinator group	Exclusive	Main*	Secondary or indistinct	Total
Small bees §	12 (11.3%)	21 (19.8%)	38 (35.9%)	71 (67.0%)
Wasps	7 (6.6%)	15 (14.2%)	26 (24.5%)	48 (45.3%)
Large bees §	8 (7.6%)	18 (17.0%)	10 (9.4%)	36 (34.0%)
Syrphids	3 (2.8%)	12 (11.3%)	18 (17.0%)	33 (31.1%)
Other flies	0	3 (2.8%)	26 (24.5%)	29 (27.3%)
Butterflies	0	2 (1.9%)	23 (21.7%)	25 (23.6%)
Beetles	0	0	13 (12.3%)	13 (12.3%)
Hummingbirds	5 (4.7%)	0	0	5 (4.7%)

* Includes plant species that have multiple pollinator groups but only one or two are the main pollinator group(s) (see methods section of text).
§ *Apis mellifera* not included.

B. POLLINATOR AGENTS

A wide array of pollinator agents were recorded (Tables 3, 4). Hymenopterans, followed by dipterans, were the most important pollinators, and all insect groups except large bees were found more often as secondary agents than as exclusive or main pollination agents (Table 5). Hummingbirds, which were the only vertebrate group, acted as exclusive pollinators (Table 5).

Hymenoptera. Bees and/or wasps were among the pollinator agents of 98 of the 101 plant species pollinated by insects. In addition, hymenopterans were the pollinators of three-fourths of the plants pollinated by one group only (Table 5). We recorded at least 54 native species of bees (Table 3). The families Apidae (including "Anthophoridae"), Halictidae, and Megachilidae were represented by 28, 16, and 8 species, respectively. Andrenidae and Colletidae were only represented by one species each. Halictidae bees—owing mainly to Augochlorini species—pollinate about half of the species in this community. Meliponini bees played a minor role in pollination, occasionally pollinating some generalist plant species, and acted more as pollen thieves in several species (e.g., *Baccharis* and Melastomataceae species, Fig. 1I). However, *Melipona bicolor*—which is markedly larger than other Meliponini bees in that area—was an important pollinator of several species (Fig. 1B, Table 3). Small and large bees belonging to Megachilidae pollinated 12 species from six families. The large Apidae bees belonging to the genera *Bombus*, *Xylocopa* Latr., and *Centris* Fabr. also were important pollinators in the community. The three bumblebee species—mainly *Bombus atratus*—pollinated at least 29 species, and they were either the most frequent or the exclusive pollinators of 12 of them. We recorded at least 46 species of wasps acting as pollinators, the most important of which were the social Vespidae, in particular *Polistes* Latr. species, followed by Pompilidae and Sphecidae.

The introduced honeybee, *Apis mellifera*, acted as a pollen robber in *Sinningia allagophylla* but pollinated the other 31 species they visited (Table 3). These bees were frequent visitors to some species classified as having bee nectar-flower pollination systems (i.e., pollinated by bees in search of nectar; see "Pollination Systems" below), such as *Ilex amara*, *Gaylussacia chamissonis*, *G. jordanensis*, and *Cuphea glutinosa*. Honeybees were the most important pollinators of the three *Hyptis* Jacq. species (Lamiaceae) and the only flower visitor for the other Lamiaceae, *Peltodon radicans*.

Diptera. Syrphids constituted a noticeable group of pollinators in the community, feeding on both nectar- and pollen-flowers. Species of the genus *Toxomerus* Macq. were particularly important and, for instance, *T. watsoni* acted as a pollinator of 21 species (Table 3). Flies other than syrphids were represented mainly by Tachinidae and Bombyliidae (beeflies) and, usually, were secondary or indistinct pollinators of polyphilous or holophilous species (Fig. 2B, Tables 5, 6).

Lepidoptera. Pollination by lepidopterans (Fig. 2I) was poorly represented. Butterflies ("Rhopalocera") and diurnal moths ("Heterocera") generally played a secondary role for plants pollinated mainly by bees (Tables 4, 5, 6). They were among the most frequent pollinators of only a few Asteraceae species. Butterflies belonging to the genus *Vanessa* Fabr. (Nymphalinae) were the most frequent flower visitors of this group. In spite of the scarcity of their visits to flowers, many butterflies were recorded during the summer and fall, and small butterflies belonging to Hesper-

Figure 1. Flowers and pollinators at the Serra da Bocaina grasslands. A–C. Bee nectar-flowers. —A. *Augochloropsis* aff. *cognata* (Halictidae) visiting a flower of *Pavonia kleinii* (Malvaceae). —B. A stingless bee *Melipona bicolor* (Apidae) entering a bell-shaped flower of *Gaylussacia chamissonis* (Ericaceae). —C. *Bombus brasiliensis* (Apidae) visiting a head of *Vernonia westiniana* (Asteraceae). D, E. Wasp/fly flowers. —D. *Polistes billardieri* (Vespidae) visiting a head of *Gochnatia paniculata* (Asteraceae), which is also pollinated by syrphids. —E. *Polybia sericea* (Vespidae) visiting a flower of *Gonioanthela hilariana* (Apocynaceae). F–J. Bee pollen-flowers. —F. A flower of *Tibouchina minor* (Melastomataceae). Note the long poricidal anthers. —G. *Augochloropsis* sp. indet. 1 collecting pollen by vibration from a single anther of a *Trembleya phlogiformis* (Melastomataceae) flower. This bee only occasionally touches the stigma (arrow). —H. *Bombus atratus* collecting pollen by vibration in *Trembleya phlogiformis*, which is mainly pollinated by this bee. —I. *Paratrigona subnuda* (Apidae) collecting pollen from a flower of *Trembleya parviflora*. This bee removes pollen from the anther by inserting its proboscis and acts as pollen thief since it does not transfer pollen to the stigma of this species, which is pollinated by another stingless bee, *Melipona bicolor*. —J. *Megachile iheringi* (Megachilidae) collecting pollen from a keel shaped flower of *Lupinus velutinus* (Leguminosae). Note the bee abdomen touching the keel petals (arrow). K, L. Syrphid/small bee pollen-flowers. —K and L. Syrphids species feeding directly on pollen from flowers of *Xyris tortulla* (Xyridaceae) and *Calydorea campestris* (Iridaceae), respectively. See Table 2 for flower measurements.

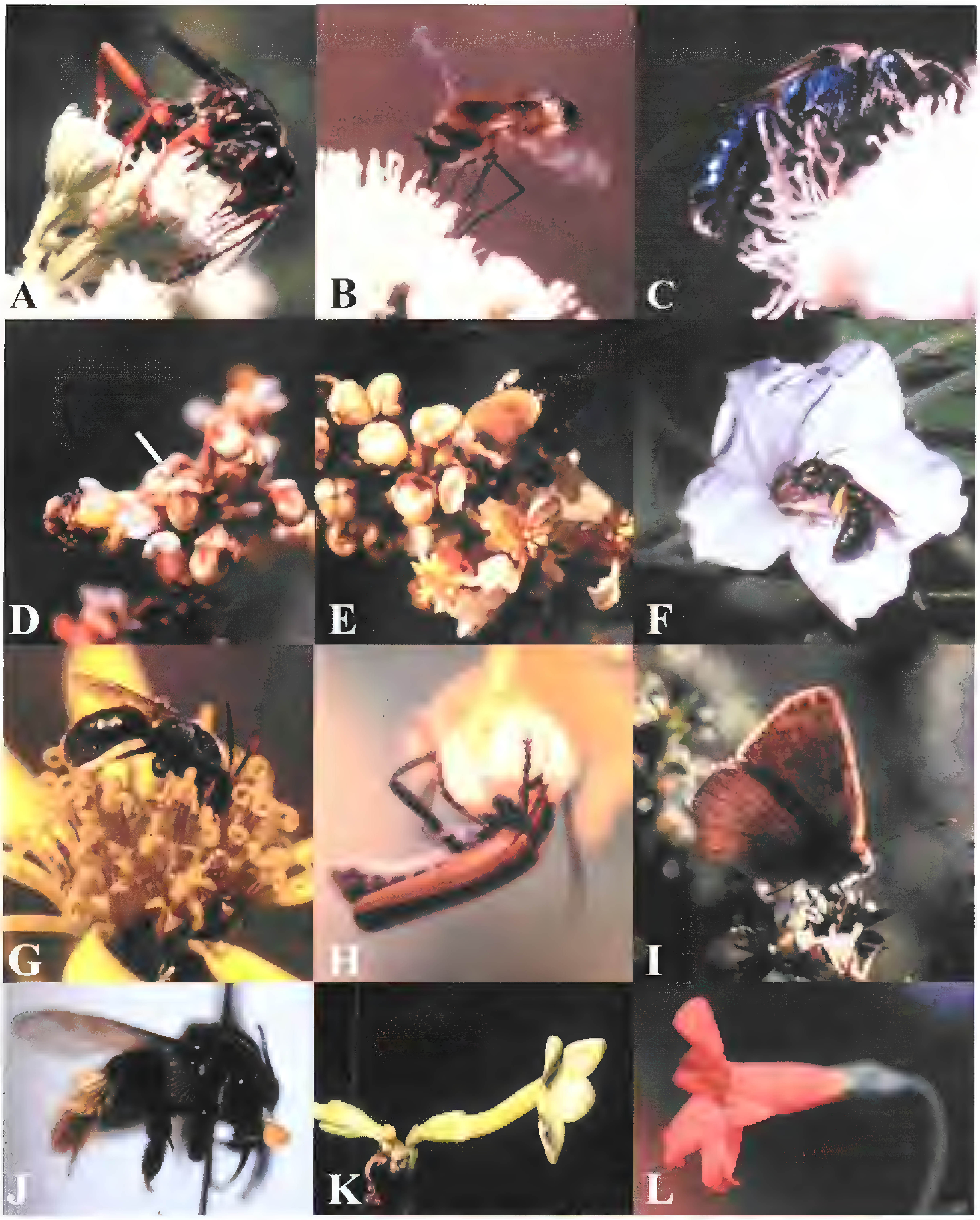

Figure 2. Flowers and pollinators in the Serra da Bocaina grasslands. Flowers pollinated by several insect groups: —A–C. Species of three pollinator groups visiting the heads of *Eupatorium* sp. indet. 1 (Asteraceae), respectively, a wasp (*Sphex opacus*, Sphecidae), a beefly (Bombyliidae), and a small bee (*Augochloropsis cyanea*, Halictidae). Oil-flower: —D. *Paratetrapedia* sp. indet. 1 collecting pollen from flowers of *Byrsonima variabilis* (Malpighiaceae). Note the flower oil-glands or elaiophores (arrow). —E. *Centris* cf. *insularis* (Apidae) collecting oil from flowers of *Byrsonima variabilis* (Malpighiaceae). Syrphid/small bee nectar-flowers: —F. *Ceratina* sp. indet. 2 (Apidae) visiting a flower of *Convolvulus crematifolius* (Convolvulaceae). —G. *Pseudagapostemon cyaneus* (Halictidae) visiting a head of *Senecio oleosus* (Asteraceae). Minor pollinator groups: —H. A beetle (Cantharidae sp. indet. 2) visiting a flower of the mainly wasp-pollinated *Clethra scabra* (Clethraceae). —I. A butterfly, *Thecla* sp. indet. 1 (Lycaenidae), visiting the generalist flowers of *Galianthe brasiliensis* (Rubiaceae). Doubtful pollination systems: —J. A female *Monoeca* sp. indet. 1 (Apidae) with a pollinarium of a species of *Oncidium* (Orchidaceae) attached to its clypeus. This digger bee was captured while collecting oil on flowers of *Byrsonima variabilis*, and its role in the pollination of *Oncidium* species is uncertain. —K. Flower of *Helia oblongifolia* (Gentianaceae). Floral traits point to pollination by nocturnal moths, but no pollinators were observed. —L. Flower of *Calolisianthus pedunculatus* (Gentianaceae). The attractive flowers of this species seem to be adapted to pollination by hummingbirds, but they are nectarless and spontaneously self-pollinated. See Table 2 for flower measurements.

Table 6. The number (and percentage) of plant species that are monophilous (most specialized), oligophilous, polyphilous, and holophilous (most generalized) within each pollination system and pollinator group at the Serra da Bocaina grasslands.

	Monophily	Oligophily	Polyphily	Holophily	Total of species†
All species	36 (34.0%)	32 (30.2%)	18 (17.0%)	20 (18.8%)	106
Pollination system					
Small and large bee nectar-flowers*	10 (33.3%)	12 (40.0%)	8 (26.7%)	0	30
Wasp and wasp/fly nectar-flowers	7 (36.4%)	8 (31.8%)	7 (31.8%)	0	22
Several insect groups	0	0	0	20 (100%)	20
Small and large bee pollen-flowers	11 (73.3%)	3 (20.0%)	1 (6.7%)	0	15
Syrphid and syrphid/small bee pollen-flowers	2 (22.2%)	6 (66.7%)	1 (11.1%)	0	9
Hummingbird flowers	5 (100%)	0	0	0	5
Syrphid/bee nectar-flowers	0	2 (66.7%)	1 (33.3%)	0	3
Small and large bee oil-flowers	0	1 (100%)	0	0	1
Syrphid nectar-flowers	1 (100%)	0	0	0	1
Undetermined or uncertain	—	—	—	—	18
Pollinator groups§					
Small bees ‡	12 (16.9%)	25 (35.2%)	16 (22.5%)	18 (25.4%)	71
Wasps	7 (14.6%)	11 (22.9%)	14 (29.2%)	16 (33.3%)	48
Large bees ‡	8 (22.2%)	12 (33.3%)	10 (27.8%)	6 (16.7%)	36
Syrphids	3 (9.1%)	10 (30.3%)	9 (27.3%)	11 (33.3%)	33
Other flies	0	3 (10.3%)	9 (31.1%)	17 (58.6%)	29
Butterflies	0	3 (12.0%)	6 (24.0%)	16 (64.0%)	25
Beetles	0	0	2 (15.4%)	11 (84.6%)	13
Hummingbirds	5 (100%)	0	0	0	5

† Does not include species where the pollination system was not determined or was uncertain.
* Includes *Gaylussacia chamissonis* and the four species of Lamiaceae pollinated exclusively or mainly by *Apis mellifera*.
§ Since many species are pollinated by more than one pollinator group, the sum total of plant species exceeds 106.
‡ *Apis mellifera* not included.

iinae (probably species of *Corticea* Evans) were very common in all seasons at the study sites.

Coleoptera. Beetles pollinated a few species and always acted as secondary or indistinct pollinators (Tables 5, 6). Cantharidae (Fig. 2H), most particularly Cantharidae sp. indet. 1, which pollinated 10 species (Table 3), was the only beetle family with a notable importance in pollination at the community level.

Vertebrata. The interactions between hummingbird-pollinated plants and their agents were the most specialized at the community level. We recorded five Trochilinae species in the study areas (Fig. 3, Table 3). These species could be observed year-round in the high-altitude forest and grasslands, except *Colibri serrirostris*, which seems to migrate to the highlands during the wet season.

Pollination Systems

The nine pollination systems differed markedly with regard to their number of species. For instance, the three most important systems, respectively, small and large bee nectar-flowers, wasp and wasp/fly nectar-flowers, and several insect groups, encompass 72 species (68% of the 106 species total; Table 6). On the other hand, two of the systems, respectively small and large bee oil-flowers and syrphid nectar-flowers, only comprise one species each (Tables 4, 6).

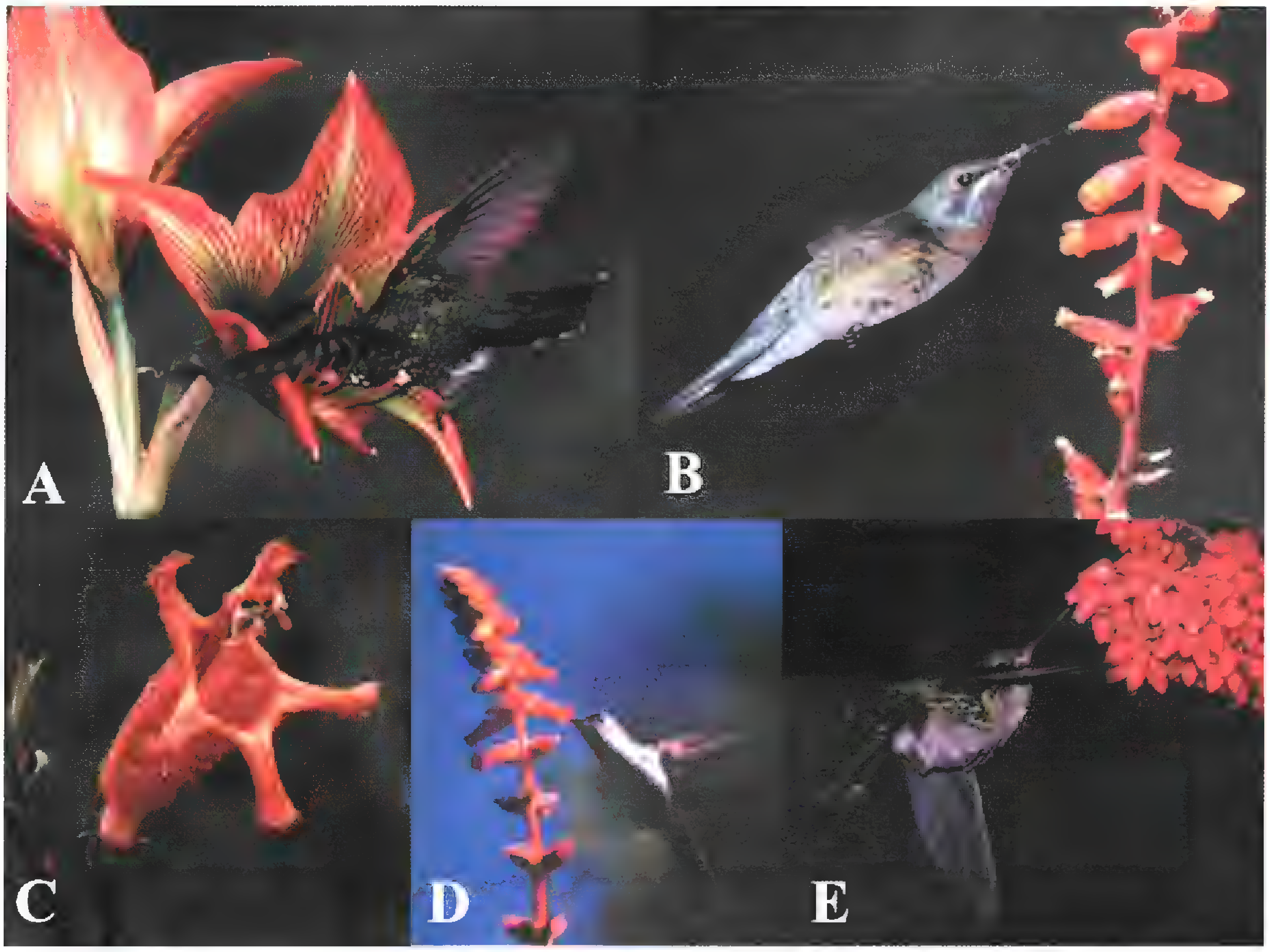

Figure 3. Hummingbirds and their flowers in the Serra da Bocaina grasslands. —A. *Leucochloris albicollis* visiting a very large flower of *Hippeastrum glaucescens* (Amaryllidaceae). Note the hummingbird's foot gripping the inferior tepal. —B. A female *Colibri serrirostris* visiting flowers of *Dyckia tuberosa* (Bromeliaceae). Note pollen on the bird's bill and forehead. —C. Flower of *Esterhazya macrodonta* (Orobanchaceae), which is pollinated by *L. albicollis*. —D. A female *Stephanoxis lalandi* visiting flowers of *Sinningia allagophylla* (Gesneriaceae). —E. A female *Chlorostilbon aureoventris* visiting flowers of *Agarista hispidula* (Ericaceae); originally published by Plant Systematics and Evolution, 2006, Springer-Verlag; reproduced with permission. See Table 2 for flower measurements.

A. NECTAR-FLOWERS POLLINATED MAINLY BY SMALL AND LARGE BEES

Plants of this group had flowers pollinated mainly by large or small bees that were searching for nectar (Fig. 1A–C). This group shows great variability in floral traits, and we observed specific associations with pollinators among its species. As a whole, this group is the most representative pollination system of the community (Table 6).

This plant group first includes five species pollinated exclusively by small bees. Species of Malvaceae (Fig. 1A) and Polygalaceae were pollinated by Ceratinini or Halictidae bees, and *Escallonia farinacea* was pollinated only by *Colletes* sp. indet. 1 (Colletidae) (Table 4). An important sub-group comprises species predominantly pollinated by small bees, in which wasps either were rare—*Mikania lundiana*, *Hyptis umbrosa*, and *Gaylussacia jordanensis*—or acted as secondary agents—*Ilex amara* and *Gaylussacia chamissonis* (Fig. 1B). The last three species have white, bell-shaped flowers.

Large bees were the exclusive pollinators of the large flowers of *Ipomoea procumbens* and *Oxypetalum sublanatum*, and also, of two Asteraceae species, *Chromolaena* cf. *decumbens* and *Vernonia* cf. *rosea*. Likewise, *Lobelia camporum* and *Hyptis lippioides* were mainly pollinated by large bees, although small bees acted as their secondary pollinators. Despite their typically melittophilous flowers (sensu Faegri & van der Pijl, 1979), *Cuphea glutinosa* and *Verbena hirta* were each pollinated by five different agents, of which large bees were by far the most frequent ones; for *C. glutinosa*, the pollen load deposited on the stigmas in a single large bee visit was significantly higher than that deposited by small bees, wasps, or syrphids (L. Freitas, unpubl. data). Both *C. glutinosa* and *V. hirta* bloom continuously (Table 1) and are among the most common plants in the study area.

Plant species pollinated by large bees produced larger quantities of nectar than the other insect-pollinated species, which typically secreted less than 2 μl of nectar per flower per day. *Oxypetalum sublanatum* and *Lobelia camporum* flowers, for instance, secreted 5.5–8 μl (n = 10) and 4–7 μl (n = 17) of nectar per day, respectively.

Another sub-group in this system is composed of species in which both large and small bees seemed to be the main pollinators—*Hypochaeris*

gardneri, *Vernonia herbacea*, *V. tragiaefolia*, *Jacquemontia grandiflora*, *Hyptis plectranthoides*, *Crotalaria breviflora*, and *Declieuxia cordigera*. The pollination systems of some species of Asteraceae diverge slightly from this last sub-group, because, in addition to small or large bees as their main pollinators, butterflies were either important agents—*Eupatorium* sp. indet. 3 and *Vernonia westiniana* (Fig. 1C)—or secondary agents—*Eupatorium* sp. indet. 1 and *V. tomentella*.

B. NECTAR-FLOWERS POLLINATED EITHER BY WASPS OR BY WASPS AND DIPTERA

This group includes species from several families, such as *Gonioanthela hilariana* (Fig. 1E), *Oxypetalum appendiculatum*, *Erythroxylum microphyllum*, *Croton dichrous*, *Clethra scabra* (Fig. 2H), and *Borreria tenella*, for which wasps were either the exclusive pollinator or the main pollinator, usually associated with flies. Wasps were also either the main or the exclusive pollinators of many Asteraceae, e.g., *Achyrocline satureioides*, *Gochnatia paniculata* (Fig. 1D), *Lucilia lycopodioides*, and *Mikania nummularia*, and of all species of the genus *Baccharis* except *B. tarchonanthoides* and *B. dracunculifolia*. In the latter, as well as in *Mikania sessilifolia* and the spontaneously self-pollinated *Galium hypocarpium*, pollination by flies and wasps was equally important.

Flowers of this group typically have easily accessible nectar and are usually greenish. Predominant flower shapes are short tube (e.g., *Mikania* Willd.) and dish (e.g., *Gonioanthela* Malme and *Erythroxylum* P. Browne), but flowers may be large in width, allowing the insect to enter and reach the nectar (e.g., *Oxypetalum appendiculatum*). Wasps carry few pollen grains on their bodies, and some species belonging to this pollination system may be additionally pollinated by wind.

C. POLLEN-FLOWERS POLLINATED BY SMALL AND LARGE BEES

Nectarless flowers with poricidal anthers are the most characteristic of this system, which includes species of Melastomataceae and Solanaceae, among others (Fig. 1F–I). Plants of this group were pollinated by large and small bees, which collected pollen by vibration. Large Apidae bees—belonging to the genera *Bombus*, *Xylocopa*, and *Centris*—were the exclusive pollinators of *Tibouchina frigidula*, *T. martialis*, and *Chamaecrista* sp. indet. 1. Large bees were also the pollinators of *Tibouchina minor* (Fig. 1F), *Trembleya phlogiformis* (Fig. 1G–H), and *Ouratea semiserrata*, in addition to such small bees as *Melipona bicolor* and some Halictidae species. The remaining plant species with poricidal anthers—*Trembleya parviflora* (Fig. 1I) and the five *Solanum* L. species—have relatively small flowers, which were only pollinated by small bees. Four species of *Solanum* were exclusively pollinated by the same small bee—*Augochloropsis cyanea* (Halictidae). This bee (Fig. 2C) is endemic to the Brazilian coastal range and is markedly larger (mean body length 10.1 ± 0.99 mm, n = 10) than other Halictidae species in the study area.

Bees searching for pollen also pollinated some flowers without poricidal anthers. *Viola cerasifolia* flowers have five anthers opening longitudinally, but their androecium is arranged so as to function as a single poricidal anther. This species was mainly pollinated by small *Anthrenoides* Ducke bees (Andrenidae), which showed a singular pollen collecting behavior on these flowers, in addition to vibration (see Freitas & Sazima, 2003a for details).

The nectarless flag-shaped flowers of *Lupinus velutinus* were only pollinated by large bees belonging to the genera *Bombus* and *Megachile* Latr. (Fig. 1J). During the bumblebee visits, the weight of the bee flexed the wing petals downward and pollen was therefore pressed out in portions, at the tip of the keel ("macaroni pump" type of pollen presentation, sensu Endress, 1994), which contacted the abdomen of the bee. However, pollen collection by bumblebees was usually improved by vibration. Leafcutter bees seem to lack the necessary weight to flex the wings and press pollen out of the keel. During their visits to a flower, these bees used their head as a lever, and the wings were thus depressed by their front and middle legs (Fig. 1J). The hind legs stroked the sides of the keel, forcing a stream of pollen out of the keel beak, and pollen was then packed on the ventral abdomen of the bee ("milking action," sensu Wainwright, 1978).

Bombus atratus, collecting pollen by vibration, was the effective pollinator of *Alophia geniculata* flowers, although its visits were infrequent. Small bees and syrphids frequently fed on pollen of this species, but they only occasionally pollinated its large flowers. A similar pollination system is expected for *Alophia* sp. indet. 1, although we were unable to record any large bees on its flowers (Table 4).

D. POLLEN-FLOWERS POLLINATED EITHER BY SYRPHIDS OR BY SMALL BEES AND SYRPHIDS

Syrphids were the exclusive pollinators of *Drosera montana* and *Deianira nervosa* and the co-pollinators, in association with small bees, of *Zygostigma australe*, *Calydorea campestris*, *Sisyrinchium vaginatum*, *Xyris asperula*, and *Xyris tortulla* (Fig. 1K–L). Species in this group typically bear small, dish-shaped, actino-

morphic, and vividly colored pollen-flowers. Pollen grains are easily accessible to pollinators of these species because their anthers open longitudinally. Flowers of *Sisyrinchium micranthum* bear oil-secreting trichomes at the base of the staminal column (see Cocucci & Vogel, 2001, Truylio et al., 2002). However, we failed to detect any oil-collecting bees on these flowers, which were pollinated by syrphids and small pollen-collecting bees.

E. NECTAR-FLOWERS POLLINATED BY SEVERAL INSECT GROUPS (SIG)

This group contains species pollinated by three or more functional groups with similar importance (holophily). The SIG system includes some species with very small, greenish flowers—*Eryngium horridum* (and probably *E. canaliculatum*), *Paepalanthus paulensis*, *P. polyanthus*, and *Weinmannia organensis*—that fit the "diverse small insects" (d.s.i.) syndrome of Bawa et al. (1985).

The SIG system also includes species from several Asteraceae genera (*Baccharis tarchonanthoides*, *Barrosoa betoniciiformis*, *Campuloclinium megacephalum*, *Chaptalia integerrima*, *C. runcinata*, *Eremanthus erythropappus*, *Erigeron maximus*, *Eupatorium* sp. indet. 2, *Eupatorium* sp. indet. 4 [Fig. 2A–C], *Grazielia gaudichaudeana*, *Stevia myriadenia*, *Symphyopappus compressus*, *and Vernonia megapotamica*) and three Rubiaceae species (*Borreria capitata*, *Galianthe angustifolia*, *and G. brasiliensis* [Fig. 2I]). Large insects, such as bumblebees and Pompilidae wasps, were among the pollination agents of some holophilous species of Asteraceae and Rubiaceae, which thus differed from the species of Apiaceae, Eriocaulaceae, and Cunoniaceae, which have very small flowers (Table 4).

F. HUMMINGBIRD POLLINATED FLOWERS

Hummingbirds were the exclusive pollinators of five species from five families. These species bear tubular/urceolate flowers that make them easily distinguishable from flowers of other species in this community (Fig. 3). Except the nectarless, spontaneously self-pollinated flowers of *Calolisianthus pedunculatus* (Fig. 2L), all species with red-orange flowers were pollinated by hummingbirds.

Each of these plant species was pollinated by one to four hummingbird species (Tables 3, 4). *Leucochloris albicollis* was the main visitor in the study area, pollinating four species and acting as the single pollinator of *Esterhazya macrodonta* and *Hippeastrum glaucescens*. This *Hippeastrum* Herb. species bears very large flowers (tepals ca. 140 cm long), and the birds needed to perch on one of the inferior tepals to reach the nectar at the flower base (Fig. 3A). Pollen was deposited mainly on their wings. On the other hand, *Esterhazya macrodonta* has protandrous flowers (Fig. 3C) that last up to six days. Nectar removal in the first days of anthesis strongly affects nectar production (see Freitas & Sazima, 2001 for details).

Sinningia allagophylla bears a long hairy inflorescence with more than 40 flowers, which last up to seven days and present partial herkogamy associated with protandry. This gesneriad was mainly pollinated by *Leucochloris albicollis* and *Stephanoxis lalandi* (Fig. 3D), but also by *Colibri serrirostris* and *Clytolaema rubricauda*. The flower disposition along the inflorescence of *Dyckia tuberosa* resembles that of *S. allagophylla* (Fig. 3B, D), and we only observed *Colibri serrirostris* females pollinating this terrestrial bromeliad (Fig. 3B). *Agarista hispidula* bears dozens of flowers arranged in dense inflorescences (Fig. 3E). Flowers are urceolate with poricidal anthers, and pollen is secondarily presented on hairs at the corolla opening. It was pollinated very early in the morning, mainly by the small *Chlorostilbon aureoventris* (Fig. 3E), but also by *Leucochloris albicollis* (see Freitas et al., 2006 for details). In general, ornithophilous species were rare in these grasslands. We found only four, seven, and eight flowering individuals of, respectively, *Agarista hispidula*, *Dyckia tuberosa*, and *Hippeastrum glaucescens* in the study areas. It was common for there to be < 10 *Esterhazya macrodonta* plants along each 1 km transect; however, along one exceptional transect we found 55 flowering individuals, whose nectar features were also studied (Freitas & Sazima, 2001). In contrast, *S. allagophylla* was common in many places in the Serra da Bocaina. Individuals of this species were usually distributed in small clusters (three to eight plants) separated from each other by many meters. However, *S. allagophylla* plants occurred in large clusters in some areas—with dozens of individuals per 100 m^2—probably due to clonal reproduction. *Esterhazya* Mikan., *Agarista* D. Don. and *Dyckia* Schult. f. plants were rarely visited, receiving, respectively, 0.05, 0.18, and 0.20 visits per hour (see Table 4 for times of observation). Each plant of *Hippeastrum glaucescens* received ca. one visit every two hours. Although plants of *Sinningia* Nees growing in small clusters received ca. only one visit every three hours, when in large clusters, hummingbirds visited each patch between three and six times per hour so that most individuals were visited at intervals of one to two hours.

Because of the low flower availability, hummingbird species basically acted as low-reward trapliners in the studied grasslands (foraging strategies after Feinsinger & Colwell, 1978). Territorial foraging behavior was recorded only in the large clusters of

Sinningia allagophylla. *Clytolaema rubricauda* and *Stephanoxis lalandi* behaved territorially in these circumstances, and *Leucochloris albicollis* occasionally acted as a parasite in territories set by *Clytolaema rubricauda*. Thus, *Leucochloris albicollis* may alternate its foraging strategy from low-reward traplining to territory-parasitism in some cases.

G. MISCELLANEA

Many oil-collecting bees—mainly large bees belonging to *Centris*—were recorded pollinating *Byrsonima variabilis* (Fig. 2D–E). The mechanism for oil-collection in this species was similar to that recorded for other Malpighiaceae species (see Vogel, 1990). *Byrsonima variabilis* was also pollinated by small bees belonging to Apidae (Meliponinae) and Halictidae in search of pollen, but to a minor degree. Some oil-collecting bees also collected pollen on this *Byrsonima* Rich. ex Juss. species.

The nectar-flowers of *Tassadia subulata* were exclusively pollinated by syrphids, which carried the pollinia on their heads. The elaborate, small, ruby flowers of this species are typically myophilous (sensu Faegri & van der Pijl, 1979). Small bees were also associated with syrphids on the nectar secreting flowers of *Senecio oleosus*, *Wahlenbergia brasiliensis*, and *Convolvulus crenatifolius* (Fig. 2F–G). The last two species bear bell-shaped, lilac/lavender flowers. Pollinators first fed on the nectar of these three species, although they also searched for pollen on them. Syrphids and small bees seemed to be co-pollinators of these species (syrphid/bee nectar-flower system).

H. SPECIES WHOSE POLLINATION SYSTEMS ARE DOUBTFUL

The flowers of 18 species were either not visited during the observation sessions or the role of their visitor in pollination was not clear. The results and brief discussions of these cases are presented herein.

Although many *Oncidium* Sw. species bear flowers that produce nonvolatile oils with a chemical composition suitable for larval nurturing by "Anthophoridae" bees (Reis et al., 2000; A. D. Faria, pers. comm.), only one single observation of a bee actively collecting oils on *Oncidium* flowers has been reported so far (Singer & Cocucci, 1999). We did not observe oil-collecting bees visiting flowers of *Oncidium* species (total 47 hr. of observation, Table 4). However, we collected an individual of *Monoeca* sp. indet. 1 (Tapinotaspidini) (Fig. 2J) and an individual of *Megachile aureiventris* Schrottky (Megachilidae) each carrying an *Oncidium* pollinarium attached to its head. During an observation session on *Lupinus velutinus* flowers, a female individual of *Bombus*—after collecting the pollen of *Lupinus* L. flowers—quickly visited a flower of *Oncidium barbaceniae*. During this visit, the bee vibrated in a failed attempt to collect pollen. We did not collect this individual bumblebee but observed that the visited flower had no pollinia, indicating that this bee could have removed them. These observations indicate that bees in search of pollen could be acting as pollinators in these populations of *Oncidium*. Thus, in addition to the expected system involving oil-collecting bees, *Oncidium* flowers could be pollinated by deceit by pollen-collecting bees. The following aspects point to a pollination system by deceit in the studied populations: (1) bees in search of pollen visited their flowers; (2) bees of the "Anthophoridae" group intensively collected oil on *Byrsonima* flowers but were not recorded on flowers of the *Oncidium* species growing in the same patch; (3) visits by bees from any group were scarce on *Oncidium* flowers, and fruit production was very low in the three species. In short, pollination of the three species at Bocaina is unclear, and more comprehensive studies are required to understand the pollination biology of this genus.

The tubular flowers of *Calolisianthus pendulus* do not produce floral nectar, except for some rare flowers with minute nectarioles (sensu Vogel, 1998) located on petals. No visits to their flowers were recorded, and delayed self-pollination seems to ensure the reproduction of this species, as well as that of the other four studied gentians of Bocaina, which include the ornithophilous *Calolisianthus pedunculatus* with nectarless flowers (Fig 4L) (see Freitas, 2004 for details).

Although the floral features of three species (*Mandevilla erecta*, *Habenaria parviflora*, and *Helia oblongifolia* [Fig. 2K]) point to phalaenophily and sphingophily (after Faegri & van der Pijl, 1979), no nocturnal moths were recorded visiting their flowers (Table 4). These species flower in the middle of the wet season (Table 1). The flowers have narrow greenish or yellowish tubes (spurs in *H. parviflora*), presenting both odor and nectar at night. The long-lived flowers of *H. oblongifolia* are spontaneously self-pollinated at the end of anthesis (Freitas, 2004). The other two species were rare in the studied areas. *Mandevilla erecta* bears large inflorescences with dozens of flowers, but we only recorded one fruit produced during three subsequent blooming seasons (from 1998 to 2000). Several *Habenaria parviflora* plants produced fruits in the study areas. Although this species is self-compatible, spontaneous self-pollination is improbable (Singer, 2001). It is pollinated by crepuscular crane-flies and nocturnal moths in an area at sea level by the São Paulo

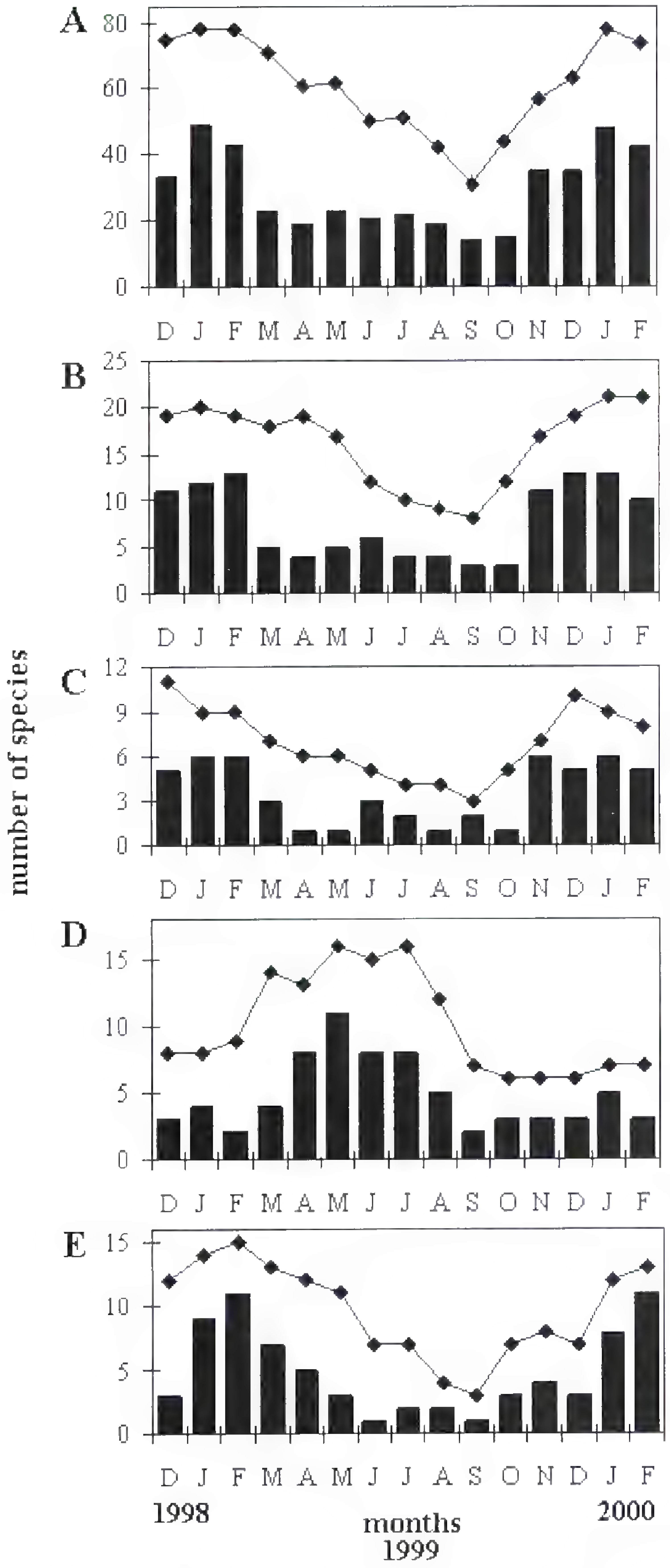

Figure 4. Number of species blooming (line) and in flowering peak (bars) from Dec. 1998 to Feb. 2000, in the Serra da Bocaina grasslands. —A. Distribution at the community level (n = 124). —B–E. Distribution of plant species of each pollination system. —B. Nectar-flowers pollinated mainly by small and large bees (n = 30). —C. Pollen-flowers pollinated by small and large bees (n = 15). —D. Nectar-flowers pollinated either by wasps or by wasps and dipterans (n = 22). —E. Nectar-flowers pollinated by several insect groups (SIG) (n = 20).

coastline (Singer, 2001). Results indicate that moths seldom use floral resources from grassland plants.

The two studied species of *Hypericum* L. have extended flowering times, with individual plants flowering in different months year-round. The polyandrous flowers of both species are similar (Table 2). The flowers of the fourteen individuals of *Hypericum ternum* in the study area did not produce pollen, but all flowers developed fruits with well-developed seeds. Similar results were found for the ca. 40 individuals of *Hypericum brasiliense*. However, two individuals of the latter were found to produce flowers with pollen grains (ca. 95% viability) in December 1998. One of these plants had been followed since January 1998, and, curiously, it produced only flowers without pollen until December 1998. This capacity for sexual and apomictic reproduction within the same individual is named facultativism and may be environmentally influenced (Asker & Jerling, 1992). In the pollen-producing flowers of *Hypericum brasiliense*, self- and cross-pollen tubes grew down the style, but only crossed ones seemed to penetrate the ovule. We observed these pollen-producing individuals in December 1998 and January 1999 and found that insects, mainly syrphids and small bees, searched for pollen and pollinated their flowers (Table 4). Empty anthers were also observed in herbarium specimens of *Hypericum* species from lowland forest areas (V. Bittrich, pers. comm.). It is expected that *H. ternum* also occasionally produces pollen.

No floral visitors were registered during the 28 hr. of observation of the four *Leandra* Raddi species. There are records of apomixis and pollenless flowers in species of this genus (Goldenberg & Shepherd, 1998; R. Goldenberg, pers. comm.); thus the *Leandra* species at Bocaina may also be apomictic. Another Melastomataceae, *Microlicia isophylla*, was not visited either. This species is very common in grasslands and bears attractive flowers, with magenta petals and vivid yellow anthers. Their smooth pollen grains are highly viable and are produced in large quantity. Bees collecting pollen by vibration are the expected pollinators of this species, although it could also be apomictic.

The small, greenish flowers of *Eryngium canaliculatum* are very similar to those of *E. horridum*. Floral traits of *E. canaliculatum* point to a SIG pollination system, although only four visits by two species of beetles were recorded on these flowers. Further observations are necessary to ascertain their pollination system. We did not observe pollinators visiting the showy flowers of *Chromolaena xylorrhiza* and *Epidendrum secundum* that fit in the melittophilous syndrome.

Degree of Specialization of Pollination Systems

Around one third of the plant species were pollinated by only one pollinator group (monophilous, Table 6). For 50 out the 70 species pollinated by two

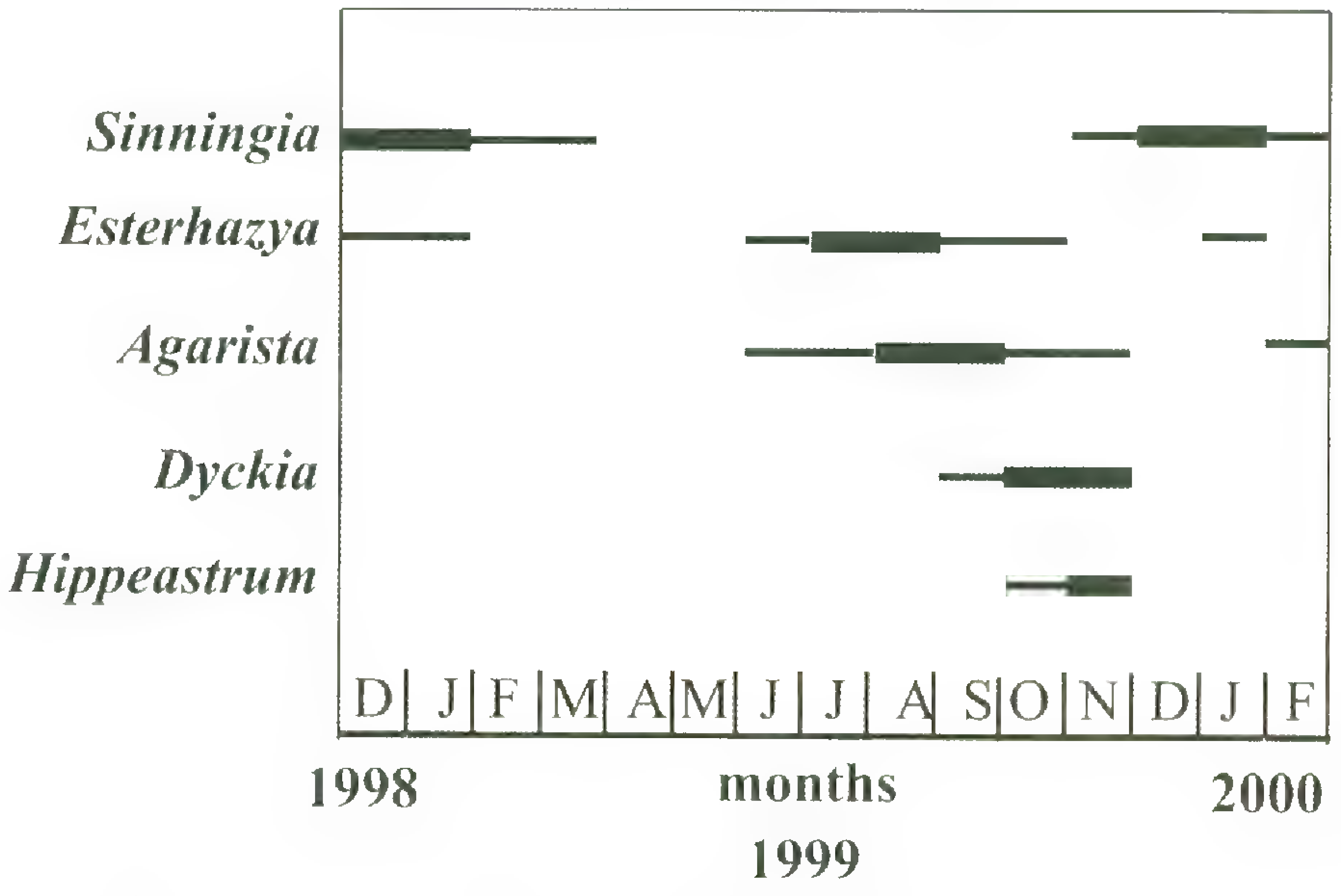

Figure 5. Flowering patterns of the five hummingbird-pollinated species from the Serra da Bocaina grasslands from December 1998 to February 2000. Thin and thick lines indicate, respectively, flowering time and flowering peak. Plant species are abbreviated according to their genus (see Table 1 for species epithet).

to six pollinator groups, we were able to determine one or two insect groups acting as main pollen vectors (oligophilous and polyphilous). The remaining 20 species were holophilous, since they presented no dominant pollinator group. Monophily dominates among pollen-bee flowers, and oligophily among syrphid and bee pollen-flowers. Species belonging to the bee nectar-flowers and wasp/fly flowers systems are more equitably distributed among monophily, oligophily, and polyphily (Table 6).

More than half of the species pollinated by small and large bees are monophilous or oligophilous (Table 6). In contrast, most species pollinated by flies, butterflies, and beetles are holophilous. The species pollinated by wasps and syrphids are better distributed among oligophily, polyphily, and holophily.

Flowering Phenology

Flowering duration in grasslands was long (mean 5.5 ± 2.92 months, n = 124), and the mean flowering peak duration was 2.6 ± 1.56 months (n = 124) (Table 1). Flowering pattern in this community was seasonal, with a peak during the middle of the wet season (Fig. 4A). Over 60% of the species flowered in January and February, and ca. one-third of the species were at their flowering peak during these two months. There was a drastic reduction in flowering during the end of the dry season/beginning of the wet season (Aug.–Oct.). The fire that occurred in one area in September 1999 may have only slightly affected these general patterns, because only eight species from this area did not occur in at least one of the other two studied areas (see Table 1).

Blooming patterns of the species with nectar- or pollen-flowers pollinated by bees followed the pattern observed in the community (Fig. 4A–C). However, there was a slight increase of species at peak flowering in June (Fig. 4B–C). In contrast, most species with nectar-flowers pollinated either by wasps or by wasps and dipterans reached their flowering peak during the dry season (Fig. 4D). Wasps are very important pollinators during that season. For example, 11 out of 23 species at their flowering peak in May, 1999 were exclusively or mainly pollinated by wasps (Fig. 4A, D). The flowering pattern of SIG species resembles the general pattern of the community, but a few plants at their flowering peak were recorded throughout the year (Fig. 4A, E). The flowering of the five hummingbird-pollinated species concentrated at the beginning of the wet season (Fig. 5). No plants flowered in April and May, and no plants were at their flowering peaks during five months of the year.

Discussion

Although Martinelli (1989) reported a total of 215 flowering species in the Bocaina grasslands, we collected ca. 260 species. About 20% of these 260 species belong to the families Poaceae, Cyperaceae, and Juncaceae and are anemophilous. This study thus included around 60% (124 species) of the ca. 210 animal-pollinated species from the Bocaina grasslands, and pollinators were determined for about half of these zoophilous species (106 species). In addition, ca. 80% of the 47 plant families found in the Bocaina grasslands were represented in this study, so that our sample was fairly representative of these high-altitude grasslands.

We carried out intensive pollinator observations for some plant species and brief ones for many others, as expected in studies on plant-pollinator interactions at

the community level which encompass many species with low population density (see Momose et al., 1998). Both the short observation times and the generally low flower visitation rates explain why we may have failed to ascertain the typical pollination system of some species in the Bocaina grasslands. However, since we used broad categories to describe the pollination systems, we may outline general interaction trends in this community and establish general comparisons.

There are no comparative data on the floral and pollination biology of any other high-altitude grassland areas in southeastern Brazil. However, community level pollination data from vegetational types with both abiotic similarities and strong biogeographic connections are available. These include the high temperate Chilean Andes, especially in the sub-Andean scrub zone (Arroyo et al., 1982), the Venezuelan Guiana high-altitude shrubland or *arbustal* (Ramírez, 1989), the Brazilian open savannas or *cerrado* (Barbosa, 1997; see also Silberbauer-Gottsberger & Gottsberger, 1988 and Oliveira & Gibbs, 2000 for other *cerrado* physiognomies), and, to some extent, data from the Brazilian *campo rupestre* (Faria, 1994). We focus our discussion on comparisons between these formations and the Bocaina grasslands.

Floral Traits

Flowers with light colors—including greenish, pink, and white color groups—are well represented in the grasslands, resembling the *arbustal* and *cerrado* communities, in which light-colored flowers predominate (Silberbauer-Gottsberger & Gottsberger, 1988; Ramírez, 1989; Barbosa, 1997). However, more than half of the species at Bocaina have showy flowers (violet, yellow, and red color groups). This dominance is due to the presence of Asteraceae and Melastomataceae, with their showy violet-colored flowers, in these grasslands. Furthermore, greenish flowers were more continuously distributed throughout the year, in contrast to violet flowers that are concentrated during the wet months. Using canonical discriminant analysis (L. Freitas, unpubl. res.), we only detected a weak relationship between floral color and the frequency of visits for each pollinator group in the community. Red flowers were strongly associated with hummingbird visitation and greenish flowers weakly associated with visitations primarily by beetles and wasps. Although we used the human color spectrum, such results for insect responses to flower color resemble the general trends detected by Chittka et al. (1994) and Waser et al. (1996), who found no statistical differences among insect pollinator groups, at the order level, in terms of the colors of the visited flowers.

The prevalence of nectar as the main floral resource at Bocaina was recorded in other grassy communities (Arroyo et al., 1982; Ramírez, 1989; Faria, 1994; Barbosa, 1997). In fact, nectar-flowers are the most important flower class among angiosperms in general, because most pollinator groups are nectar consumers (Endress, 1994). The percentage of pollen-flowers at Bocaina was similar to that registered in the *campo rupestre* (Faria, 1994) and the *cerrado* (Barbosa, 1997). Melastomataceae species are the most important pollen-flowers at Bocaina, as well as in the *campo rupestre* (Faria, 1994). Species of this family are also important pollen sources in the *arbustal* (Ramírez, 1989). However, species of other families, such as Leguminosae and Myrtaceae, constitute the chief sources of pollen in the *cerrado* (Barbosa, 1997). Malpighiaceae are represented by several species in the *campo rupestre* and the *cerrado* (Faria, 1994; Barbosa, 1997), which explains why oil-flowers are more frequent in those communities than in the Bocaina grasslands.

Although small flowers predominate in the *arbustal* and the *cerrado* (Ramírez, 1989; Barbosa, 1997), the flowers of these two communities are larger than those at Bocaina. As for the floral color patterns, the relative predominance of Asteraceae in the community strongly influences the floral size patterns. The prevalence of small tubular flowers secreting nectar at Bocaina is a direct reflection of the number of Asteraceae presenting these floral traits and apparently not the result of selection by the local pollinator agents.

The prevalence of hermaphroditic flowers is typical of angiosperms, and, consequently, characteristic of most communities (Ramírez, 1993), including the grassland flora at Bocaina. However, many of the hermaphroditic flowers exhibited spatial or temporal separation of the male and female functions, through dichogamy, herkogamy, or heterostyly. In fact, a high frequency of dichogamy (protandry) is expected in a flora dominated by Asteraceae, owing to the frequent presence of secondary pollen presentation on the style among the Asterales (see Yeo, 1993). In addition, the female ray-florets of many Asteraceae species impart a state of protogyny to the head as a whole.

All the dioecious species of the studied community belong to the genus *Baccharis*, which was primarily associated with wasp pollination. Dioecy has often been associated with a generalist mode of pollination by small opportunistic insects (Bawa, 1994; but see Renner & Feil, 1993) or with wind pollination (Culley et al., 2002). Although this study did not focus on abiotic pollination, some evidence suggests the existence of ambophily among the studied taxa, in

which wind could be a pollen vector in addition to insects (e.g., *Croton dichrous*). The species of *Baccharis* may also fit in this category, as female heads have well-exposed stigmata and male flowers produce small pollen grains. Furthermore, we found pollen grains of *Baccharis* species adhered to microscope slides covered by glycerol, during exploratory experiments at the study sites, and most species of this genus flower during the winter, when insect activity is reduced. Pollinator limitation, dry weather, and the presence of recurrent wind in the winter could favor the evolution of anemophily and ambophily in the high-altitude grasslands (see Culley et al., 2002).

Pollination Agents

Hymenopterans, markedly small bees, are the predominant pollinators in the Bocaina grasslands, as well as in the *cerrado*, *arbustal*, and Subandean zone (Arroyo et al., 1982, Ramírez, 1989; Barbosa, 1997). Bees have been reported as the main pollinators for most communities (e.g., Moldenke, 1976; Kevan & Baker, 1983; Roubik, 1989; Bawa, 1990; Momose et al., 1998; Nakano & Washitani, 2003; Ramírez, 2004), and different patterns—for example the dominance of dipterans—seem to be restricted to very singular habitats, such as Arctic and alpine areas or oceanic islands (e.g., Kevan & Baker, 1983; Primack & Inouye, 1993; Anderson et al., 2001). However, certain communities with similar percentages of bee pollination may exhibit marked differences among their general patterns of pollination. Bees belonging to different groups show great variation in, for instance, their preferences, abilities, and behavior on flowers (see Roubik, 1989), and such variation is expected to lead to different pollination patterns among communities with distinct bee faunas.

The two main functional groups of bees in the Bocaina grasslands are the large bumblebees and small halictid bees. Agents of one or both of these groups were among the pollinators of 67 out of the 106 species (63%). *Bombus* and Halictidae species pollinated, respectively, 78% of the large bee-pollinated species (28 out of 36), and 76% of the small bee-pollinated species (54 out of 71). Both bee groups exhibited a generalist foraging behavior, visiting flowers of different shapes, sizes, and colors, which, in many cases, were also pollinated by other groups. An illustrative example is that of an individual of *Bombus atratus* observed visiting the violaceous flowers of seven species, belonging to Asteraceae, Lamiaceae, and Rubiaceae, in a single foraging trip (for ca. three min). Such generalist behavior is typical of the Brazilian species of *Bombus* (Alves-dos-Santos, 1999; Barbola et al., 2000). Bumblebees pollinated most of the large bee-pollinated species at Bocaina and predominated in almost half of them, including the richest ones in terms of nectar, such as *Oxypetalum sublanatum*, *Lobelia camporum*, *Cuphea glutinosa*, and *Verbena hirta*. Moreover, these bees showed a trapline behavior, favoring pollen dispersal at great distances. Considered together, the variety of visited flowers (including nectar- and pollen-flowers), foraging behavior, dominance of the richest resources, and year-round activity make bumblebees the main pollinators of the plant group related to large bee pollination. Bumblebees are known to be one of the most important pollinators in cool temperate climates (Kevan et al., 1993; Nakano & Washitani, 2003), and the harsh climatic conditions, for a tropical place, that characterize the Brazilian high-altitude grasslands may be related to the high importance of bumblebee pollination at Bocaina.

Pseudagapostemon cyaneus (Halictidae) visited only flowers of *Mikania lundiana* and *Senecio oleosus* (Asteraceae) at Bocaina (Fig. 2G). Similarly, this bee species was a narrow oligolectic associated to *S. oleosus* flowers, in a grassland area at Lapa, State of Paraná, southern Brazil (Barbola et. al., 2000). *Pseudagapostemon cyaneus* occurs from southernmost Brazil to the State of São Paulo. In this last region, it is only reported above 1000 m (Cure, 1989). The particular interaction between *Senecio oleosus* and *Pseudagapostemon cyaneus* at both Bocaina and Lapa is one of the most illustrative examples of biogeographic connections between the mountain ranges of southeastern Brazil and the cool lowland areas in southernmost regions (see Behling, 1997).

Pollination by wasps has been observed in some highly specialized and infrequent cases (e.g., *Ophrys* L., *Ficus* L.), as well as among generalist plants pollinated by several insects (Faegri & van der Pijl, 1979). In most communities, wasps have been reported as minor agents (e.g., Arroyo et al., 1982; Bawa et al., 1985; Silberbauer-Gottsberger & Gottsberger, 1988; Momose et al., 1998; Oliveira & Gibbs, 2000). In contrast, wasps pollinated 45% of the species in the Bocaina grasslands and acted as the exclusive or main pollinators of more than 20% of the animal-pollinated species in this community (Table 5). Although wasps have their importance in the pollination of *cerrado* and *arbustal*, they are the exclusive pollinators of only a few species in these communities (Ramírez, 1989; Barbosa, 1997). In fact, as far as we know, such importance of wasp pollination as observed in the Bocaina grasslands has never been reported for any other ecosystem. Whether the wasps are minor pollinators or their role

in pollination has been neglected in Neotropical communities is still an inadequately explored issue that deserves further study. However, at least in some subtropical habitats, the rates of floral visitation by wasps, as well as their probable importance as pollinators at the community level, seem to have been underestimated (P. Feinsinger, pers. comm.).

At Bocaina, lepidopterans were generally co-pollinators of species with a generalist pollination system or secondary pollinators of species pollinated mainly by bees. Similar results were found in *cerrado* and *arbustal* areas (Ramírez, 1989; Barbosa, 1997; Oliveira & Gibbs, 2000). However, butterflies are very important pollinators in the open vegetation of the Chilean Andes, especially in the subnival zone (Arroyo et al., 1982). In spite of the scarcity of their visits to flowers, butterflies (mainly Hesperiidae) may have an important role in the gene flow of many species at Bocaina, transferring pollen at long distances due to their traplining behavior. Despite some highly specialized cases, such as those related to long-tongued flies in South Africa (e.g., Goldblatt et al., 1995), fly pollination has been considered mostly unspecialized, since flies do not feed their young and may have other food sources than flowers (Kearns, 1992; Proctor et. al., 1996). Most species pollinated by the three most important fly groups at Bocaina—Syrphidae, Tachinidae, and Bombyliidae—have small nectar-flowers that were pollinated by several agents. However, syrphids, associated with small bees, were the pollinators of many species, particularly those with pollen-flowers. These last species present monophilous or oligophilous pollination systems. This result shows that pollination by flies can be specialized even in the absence of extreme proboscis elongation. If we consider the species for which syrphids and other dipterans are either the main or the exclusive pollinator, the percentage of species pollinated by flies at Bocaina is similar to that found in *cerrado* and *arbustal* areas (Ramírez, 1989; Barbosa, 1997). Nevertheless, in the Chilean Andes, myophily is more common (Arroyo et al., 1982). The great importance of flies and butterflies in the Chilean Andes, as compared to the other communities considered here, probably reflects the unfavorable climatic conditions for bee activity in the Andes (Arroyo et al., 1982; see also Kevan, 1975 and Kearns, 1992). In the Bocaina grasslands, climatic conditions are not harsh enough to limit the development of bees, which dominate the pollination in this community.

At Bocaina, the percentage of hummingbird-pollinated species is similar to that observed in *cerrado* areas (Barbosa, 1997), but it is lower than that of other high-altitude communities, such as *arbustal* (12%) (Ramírez, 1989) and *campo rupestre* areas (10%) (Faria, 1994). In the Bocaina grasslands, ornithophilous species constitute secondary nectar sources for hummingbirds that find their main nectar sources in the surrounding high-altitude forest (Sazima et al., 1996; Freitas & Sazima, 2001). Two factors, at least, support this idea. First, in these grasslands, no ornithophilous species were flowering in April or May or were in their blooming peak during February to June. Therefore, this community would be unable to sustain hummingbirds throughout the year. Secondly, the five ornithophilous species were seldom visited by hummingbirds, while hummingbirds intensively fed on ca. 30 species of the surrounding forest areas (Sazima et al., 1996; Buzato et al., 2000; L. Freitas, pers. obs.). Hence, at Bocaina, the continued replacement of forest areas by grasslands—mainly because of fires—is a risk factor for populations of the five hummingbird species observed in the grasslands, in particular for *Stephanoxis l. lalandi*, which lives exclusively in some high-altitude areas of southeastern Brazil (Grantsau, 1989; Sazima et al., 1996).

We did not observe any pollination by either bats or other mammals in the Bocaina grasslands. Moreover, no species were collected with floral features in accordance with the mammal pollination syndromes, suggesting the absence of such pollination systems in these grasslands. Reports of bat-pollinated species from mesic habitats in high-altitude grasslands are restricted to three Bromeliaceae species (Martinelli, 1994, 1997). In contrast, bat pollination is well represented in the high-altitude forest areas that surround the grasslands (Sazima et al., 1999).

The Bocaina grasslands also lack perfume flowers, another highly specialized pollination system related to male euglossine bees (e.g., Sazima et al., 1993). Euglossine bees have restricted altitudinal limits of distribution (Roubik, 1989), and aromatic compounds traps did not detect any such bee in the Bocaina high-altitude grasslands.

In contrast to bats, nocturnal pollination by moths is expected since the Bocaina grasslands present at least three species adapted to it. However, we did not observe these pollinator agents, and the low fruit set in *Mandevilla erecta* indicate low—perhaps unpredictable—rates of flower visits by nocturnal moths in these habitats. As suggested for the *cerrado* area (Oliveira & Gibbs, 2000), strong winds at the study areas may be harmful to the moth pollinating species. In addition, the restricted flowering time of the species that might be moth-pollinated in the Bocaina grasslands may be linked to migrating pollinator agents, which would increase the difficulty of observing pollinators.

Flowering in Relation to Pollinators

At Bocaina, the bees of all families reduced their activity during the dry season. Such reduction in the number of bee species and individuals in activity during the winter was observed in connected ecosystems in southern Brazil (Alves-dos-Santos, 1999; Barbola et. al., 2000) and is related to several factors, such as the reproductive phenology of bee species, climatic restriction for flying, and flower availability. The flowering patterns of species pollinated mainly by bees followed the pattern of the community as a whole. Thus, flower resources for bees, especially large bees, decrease during the dry season. In addition, such climatic conditions as low temperatures, low precipitation, and occasional frosts are apparently unfavorable for flowering during the winter months. Moreover, the flowering pattern of species with either nectar- or pollen-flowers overlapped, and this result indicates reciprocity between the availability of resources for adults (i.e., nectar) and larvae (i.e., pollen) of bees at the community level, although it is difficult to ascertain if these patterns are not casual.

In contrast to bees, social wasps showed a more constant activity pattern throughout the year, and pollination by this group was prominent during the dry season at Bocaina. Because, in this area, several species that are pollinated mainly by wasps are apparently also pollinated by wind, anemophily, rather than pollination by wasps, may be an ultimate factor driving flowering concentration during the dry season in this group of species. If we consider the flowering phenology of species belonging to the most representative pollination systems at Bocaina, only the few species that flower during the dry season (wet season for wasp-pollinated species) seem to be fundamental to support populations of insects. For example, the floral nectar of the nearly year-long-flowering species *Cuphea glutinosa*, *Galianthe brasiliensis*, and *Verbena hirta*, and the winter-flowering *Eremanthus erythropappus* constitutes a keystone plant resource (sensu van Schaik et al., 1993) for bee pollinators during the winter. These four species are large shrubs or treelets (*E. erythropappus*) with many flowers and are particularly important for bumblebees during this period of low flower availability.

Anthropogenic fires are common during the dry season in the Bocaina grasslands. A few months after fires, we observed mass-flowering of several species such as *Sinningia allagophylla*, *Microlicia isophylla*, *Tibouchina frigidula*, *T. minor*, *Galianthe angustifolia*, and *Xyris asperulla*. Flowering controlled by fires is a well-known and widespread phenomenon among *cerrado* species (Coutinho, 1990), but, according to Safford (2001), based on his observation in the Serra do Caparaó, it is not characteristic of the Brazilian high-altitude grasslands. A possible reason for the difference between Safford's observation and ours is that the ecological similarities between *cerrado* and high-altitude grasslands may be more pronounced at Bocaina, due to intense fire regimes, than at other high-altitude grasslands of southeastern Brazil (see Safford, 1999a, 2001 and also Martinelli, 1989 for floristic comparison). In this sense, Bocaina grasslands may be more pyrogenic than other grassland areas, such as those from Pico do Itatiaia, Serra dos Órgãos, and Serra do Caparaó.

Specialist versus Generalist Pollination Systems

The traditional view in studies based on the syndrome concept (see Faegri & van der Pijl, 1979) supports the idea that pollination systems mostly tend toward increased specialization. Such a view has been questioned in more recent times due to evidence of more widespread generalization in pollination systems (e.g., McDade, 1992; Waser et al., 1996; Herrera, 1996; Ollerton, 1996; Olesen & Jordano, 2002). These field observations of regional or local flora contexts show that many plant species are visited by many animal species, and, as a result, the mean number of species of animal visitors per plant species is high. Alternatively, we used the number of functional groups of pollinators per plant species as a parameter of the degree of specialization of the pollination systems at Bocaina. Functional groups are more suited to this purpose than pollinator species for several reasons (see Fenster et al., 2004). Different species of the same functional group, for instance, are expected to exert similar selection pressures on the floral traits related to pollination mechanisms. Thus, considering such species as distinct entities generates some artificiality. Another factor is that the number of pollinator species belonging to each functional group varies drastically within a local community, as does the species richness of a given functional group among distinct communities or regions. Thus, plant species pollinated by more diverse functional groups would simply appear more generalized, despite the biological proprieties of their pollination system.

Ramírez (2002) used the functional group approach to compare the degree of specialization of nine tropical and temperate communities. The mean number of pollinator groups per plant species ranged from 1.0, in a beach dune vegetation of northern Brazil, to 1.85, in the forest of the Venezuelan Central Plain. Using the same functional groups as Ramírez (2002), the Bocaina grasslands has a mean of 2.09

pollinator types per plant, probably one of the highest values for worldwide floras. The higher degree of generalization at Bocaina is also evident if we consider the distribution of species along the four specificity categories (i.e., monophily to holophily). Monophily, as used here, encompasses both the monophily and oligophily categories of Ramírez (2002). More than half of the species, at least, belonged to these two categories in six tropical communities (between 54% and 100%; Ramírez, 2002), in contrast to the Bocaina grasslands where one third of the species are monophilous.

However, the functional group approach to determine the specialization degree of pollination systems may also induce some artificiality. One well-demonstrated theory is that different pollinators of a given plant species may vary in their pollinating abilities in such a way that this plant species may effectively specialize on its most efficient visitor (Stebbins, 1970; Schemske & Horvitz, 1984; Ollerton, 1996; Fenster et al., 2004). Another point is that the definition of functional groups of pollinators (e.g., small bees, moths, bats) is typically based on systematic boundaries. Thus, two pollinators in distinct orders are in general placed in different functional groups, even if they probably exert similar selection pressures on floral traits. For example, at Bocaina, some of the pollen-flowers are pollinated by syrphids and small bees and some of the nectar-flowers are pollinated by small bees and wasps; we named this situation oligophily. If we combine monophily and oligophily, we conclude that almost two thirds of the zoophilous species in this community present a specialization onto functional groups. Likewise, a reanalysis of the dataset from the flora of Carlinville, Illinois, indicated that about 75% of the species showed specialized pollination systems (Fenster et al., 2004), contrasting with a previous conclusion of generalization predominance in this community (Waser et al., 1996), which was based on the number of pollinator species per plant species.

Even using the above perspective of "wide functional groups" (i.e., oligophily considered as a specialized system), a considerable degree of generalization (more than one-third of species) is found in the Bocaina grasslands. Broadly, generalization is predicted as long as temporal and spatial variance in pollinator quality is appreciable; different pollinator agents do not fluctuate in unison and are similar in their pollination effectiveness (Waser et al., 1996). Thus, the climatic conditions of the high-altitude grasslands may favor the occurrence of generalists at Bocaina. Generalization in pollination systems seems to be more frequent in naturally inclement or unstable areas, in the modern agricultural-urban mosaics or human surroundings, and among short-lived plants (Vogel & Westerkamp, 1991; Johnson & Steiner, 2000, 2003). In this sense, frequent fires may be an additional factor that makes the environment harsher for specialists (both plants and animals) in the Bocaina grasslands.

Generalist pollination systems have often been characterized by small and white or greenish-colored flowers pollinated by small insects, the diverse small insect (d.s.i) syndrome of Bawa et al. (1985). However, some of the small greenish flowers at Bocaina present highly specialized pollination systems (e.g., *Gonioanthela hilariana*), and the pollination of some holophilous species involves such large insects as large bees, wasps, and butterflies. Therefore, the degree of generalization should not be inferred from the sizes of flowers and pollinators, as previously postulated by Ramírez (1989). Although represented mainly by the families Asteraceae and Rubiaceae, the holophilous species at Bocaina vary in both their floral traits and their flowering phenology. In addition, some genera with holophilous species also have monophilous or oligophilous species: for example, wasp pollination in *Baccharis* and *Borreria* G. Mey. and bee and butterfly pollination in *Vernonia* Schreb. and in the *Eupatorium* L. alliance. For such genera, the floral features that determine whether a few or several pollinator groups are attracted to the flowers of specialists or generalists, respectively, remain unclear. Moreover, since the degree of specialization/generalization of pollination systems may be influenced by factors such as plant life history, phylogenetic constraints, vegetation strata, successional status, plant abundance, breeding system, and local fauna (Stebbins, 1970; Vogel & Westerkamp, 1991; Waser et al., 1996; Ollerton, 1996; Johnson & Steiner, 2000, 2003; Ramírez, 2002, 2004; Nakano & Washitani, 2003; Fenster et al., 2004), floral traits alone may be inadequate to address this issue properly.

Concluding Remarks

The correlation between certain taxa and particular ecological conditions may enhance the abundance of given plant groups. Thus, ecological attributes, unrelated to sexual reproduction, may promote certain taxonomic groups with particular reproductive traits, and hence, may bias the frequency distribution of these traits in the community (Vogel & Westerkamp, 1991; Ramírez, 1993). Apart from the wind-pollinated species of Poaceae and Cyperaceae, the Bocaina grasslands are dominated by species of Asteraceae, which strongly influence the floral features (i.e., short tubular flowers that offer nectar and have exposed reproductive parts) at the community level. In these grasslands, general trends related to the types of

pollination systems and degree of generalization may be connected to the phylogenetic floral trends of species with certain abilities—not necessarily related to pollination—to occupy these habitats, such as short living-cycles and adaptations to frost, low mean temperature, high daily temperature variation, acidic soils, and, more recently, some kind of adaptation to fire (see Safford, 1999a).

Biogeographic and palynologic studies indicate that high-altitude grasslands in southern and southeastern Brazil have to be understood as relicts of the Pleistocene cold and dry climates and of the early- and mid-Holocene warm and dry climates (Behling, 1997). Because of their relatively recent origin, these grasslands are unlikely to have produced highly coevolved plant communities, although some relictual plant-pollinator interactions could have been retained in cases where both the plant and its pollinator colonized the mountain tops. These grasslands are linked to episodes of expansion and retraction due to glacial events during the Quaternary (Behling, 1997; Safford, 1999a). Such a situation may have favored species with the ability to occupy new habitats quickly. Dependence on a few specialized pollinators may be less suitable than more generalist pollination systems in the occupation of a new habitat, because previous pollinator agents may be left behind. In fact, generalized pollination systems may have been an ecological advantage for plants colonizing post-glacial landscapes (Johnson & Steiner, 2000, 2003). Alternatively, for those species with more specialized pollination systems, some floral traits that are frequent at Bocaina, such as spontaneous self-pollination mechanisms and long-lived flowers, may be advantageous to both plant establishment and maintenance in these grasslands characterized by unpredictable and scarce pollinators.

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EMBRYOLOGY, KARYOLOGY, AND MODES OF REPRODUCTION IN THE NORTH AMERICAN GENUS *BOECHERA* (BRASSICACEAE): A COMPILATION OF SEVEN DECADES OF RESEARCH[1]

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Abstract

The North American–Greenlandic genus *Boechera* Á. Löve & D. Löve (Brassicaceae) is distinguished from other phylogenetic lineages recognized within the artificial taxon *Arabis* L. s.l., in which it has formerly been included, by its base chromosome number *x* = 7. Based on outgroup comparisons, we consider this chromosome number to be derived from an ancestral genome comprising eight chromosomes. Chromosome counts are now available for about half of the species names listed in the most recent taxonomic treatments of the genus. An analysis of the karyological differentiation with respect to chromosome numbers was performed, and these patterns were correlated with data on pollen viability and population genetic measures in order to deduce modes of reproduction. This approach allowed us to distinguish three main groups: sexual, amphi-apomictic, and apomictic species, respectively. We focused further on the cytology of gametes, especially on that of pollen, and we discuss its role in the formation of new genotypes and cytotypes. Evidence for the following evolutionary phenomena is currently available: (1) allopolyploidization, (2) homoploid hybrid formation, and (3) establishment of viable offspring by means of fusion of highly aneuploid gametes, which resulted from irregular meiotic divisions. In contrast, there is no strict evidence demonstrating the occurrence of autopolyploidization. *Boechera* experts have just started to integrate evolutionary concepts derived from molecular analyses into taxonomic research, and profound changes, with respect to species definition and circumscription, are to be expected in the near future. The identified modes of reproduction and evolutionary phenomena will contribute to the development of a theoretical and practical basis on which future taxonomic classifications and species concepts can be based.

Key words: agamospermy, *Boechera*, Brassicaceae, chromosome number, embryology, evolution, hybridization, karyology, pollen, population genetics, speciation, taxonomy.

The genus *Boechera* Á. Löve & D. Löve (Böcher's rock cress, Brassicaceae) has recently been recognized as a monophyletic isolated lineage (Koch et al., 1999; Koch, 2003) of North American–Greenlandic distribution, based on DNA sequence variation. The genus, which according to current taxonomic treatments (Rollins, 1993; Mulligan, 1996) comprises about 80 species, was formerly included within a broadly defined genus *Arabis* L. s.l. The latter is highly polyphyletic, containing species that are to be treated within the genera *Streptanthus* Nutt. (*A. petiolaris* A. Gray; I. Al-Shehbaz, pers. comm.), *Pennellia* Nieuwl. (e.g., *A. microsperma* Rollins; Al-Shehbaz, 2003), *Arabidopsis* Heynh. (O'Kane & Al-Shehbaz, 1997; Koch et al., 1999), *Fourraea* Greut. et Burdet (*A. pauciflora* (Grimm) Garcke; Koch et al. 1991, 2001), *Pseudoturritis* Al-Shehbaz (*A. turrita* L.; Koch et al. 1999, 2001), and *Turritis* L. (*A. glabra* L.; Koch et al., 2001). Based on the occurrence of two base chromosome numbers within *Arabis* s.l., Löve and Löve (1975) proposed the splitting of this broadly distributed genus into a New World taxon (*x* = 7, *Boechera*) and a second group chiefly of Old World distribution (*x* = 8, *Arabis* s.s.). This classification is supported by several morphological characters (Al-Shehbaz, 2003).

Recently Koch et al. (2005) identified a basal phylogenetic split within the Brassicaceae based on

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the occurrence of a pseudogenic tandem repeat found in the $trnL_{(UAA)}$-$trnF_{(GAA)}$ intergenic spacer. The repeated region constitutes a synapomorphy supporting a clade comprising the cardaminoid and arabidopsoid Brassicaceae (Heenan et al., 2002), with the genus *Boechera* placed at an evolutionarily derived position. The base chromosome numbers of sister taxa (*Crucihimalaya* Al-Shehbaz, O'Kane & R. A. Price and *Capsella* Medik.) and of branches emerging deeper from its evolutionary history are primarily $x = 8$. The phylogenetic pattern of cytological differentiation shown in Figure 1 provides strong evidence that the ancient base chromosome number of the taxon, which has given rise to the cardaminoid and arabidopsoid Brassicaceae was indeed $x = 8$. This ancestral base chromosome number is furthermore supported, at least in the arabidopsoid lineage, by the high degree of collinearity between the genomes of *Capsella rubella* Reut. and *Arabidopsis lyrata* subsp. *petraea* (L.) O'Kane & Al-Shehbaz (both $2n = 16$) as has been demonstrated by Koch & Kiefer (2005) (cf. fig. 1). Consequently, the $x = 7$ condition in *Boechera* must be considered to be a derived condition resulting from chromosome reduction. Comparative map-based studies are now available that explain structural changes in plant genomes, as has been done in the case of the highly derived chromosome set ($x = 5$) of *Arabidopsis thaliana* (L.) Heynh. (Acarkan et al., 2000). Such genetic maps have not yet been constructed for *Boechera*, although several hundred microsatellite loci have been isolated and the construction of linkage maps is currently underway (T. Mitchell-Olds, pers. comm.). From recent advances in the mapping of Brassicaceae genomes (Kowalski et al., 1994; Lagercrantz, 1998; Kuittinen et al., 2004; Lysak et al., 2003, 2005), we can expect these data to provide resolution on the structural changes responsible in the origin of the distinct $x = 7$ base chromosome set characterizing *Boechera*.

The genus *Boechera* has long been known for its extensive morphological polymorphism, which is thought to have resulted from the combined evolutionary forces of hybridization, polyploidy, and apomixis (Rollins, 1966, 1983; Dobeš et al., 2004a, 2004b, 2006). However, during the past seven decades research activities have focused mainly on three taxa: *B. divaricarpa* (A. Nelson) Á. Löve & D. Löve, *B. holboellii* (Hornem.) Á. Löve & D. Löve, and the only one that is a proven monophyletic species, *B. stricta* (Graham) Al-Shehbaz (formerly *Arabis drummondii* A. Gray). Only fragmentary data on the evolutionary patterns and processes from the remaining species of this genus have been gathered.

The aim of this article is to synthesize the available data on karyology, palynology, population genetics, reproductive mode, and associated cytological pathways on a genus-wide level, with a special focus on the resulting chromosomal composition of gametes and its evolutionary significance in the establishment of new genotypes and cytotypes, respectively.

Because of the enormous taxonomic difficulties within this genus, one has to take into account that many past documentations refer to incorrectly identified material. For this reason, we are introducing a web-based gateway for ongoing *Boechera* and Brassicaceae research (<http://ephedra.hip.uni-heidelberg.de/brassicaceae>). Through this gateway, all re-examinations of vouchers referring to cytological references provided during the past seven decades will be accessible. This is also true for the summarized and discussed data of this review. In the future, we aim to open and link several other database resources on crucifer research (Ihsan Al-Shehbaz and co-workers, Michael Windham and Donovan Bailey).

Although the cytological and embryological mechanisms and phenomena addressed here may be invalid in a taxonomic context, they are applicable to evolutionary questions (i.e., they mirror evolutionary processes occurring in the genus *Boechera*). Consequently, they contribute to a theoretical and practical basis on which we can build evolutionary models and on which we can develop taxonomic and species concepts in the near future. Therefore, we recommend reading of this review in an evolutionary context, even though we, for practical reasons, have to refer to the only currently available, but highly artificial, taxonomic classification.

Somatic Chromosome Numbers

Karyological studies in *Boechera* have focused mainly on the estimation of chromosome numbers, and karyotypic analyses of their small chromosomes (3–6 μm) have recently been performed (Sharbel et al., 2004, 2005). These studies have revealed several structural peculiarities of the *Boechera* genome. For instance, Mulligan (1964: 1517) stated that diploid "native North American *Arabis*" (genus *Boechera*) species have one pair of somatic chromosomes with satellites, while triploid plants of *A. divaricarpa* A. Nelson had three somatic chromosomes with satellites. Sharbel et al. (2004) described the diploid genome of *B. holboellii* to be composed of autosomes, which have median to subterminal centromere positions.

Another conspicuous feature is the presence of aneuploid chromosomes (or chromosome fragments) that were mainly observed in *Boechera holboellii* (Table 1a and 1b) and that can be differentiated from the normal autosomes by their conspicuously smaller size (Böcher, 1947; Mulligan, 1964; Packer, 1964;

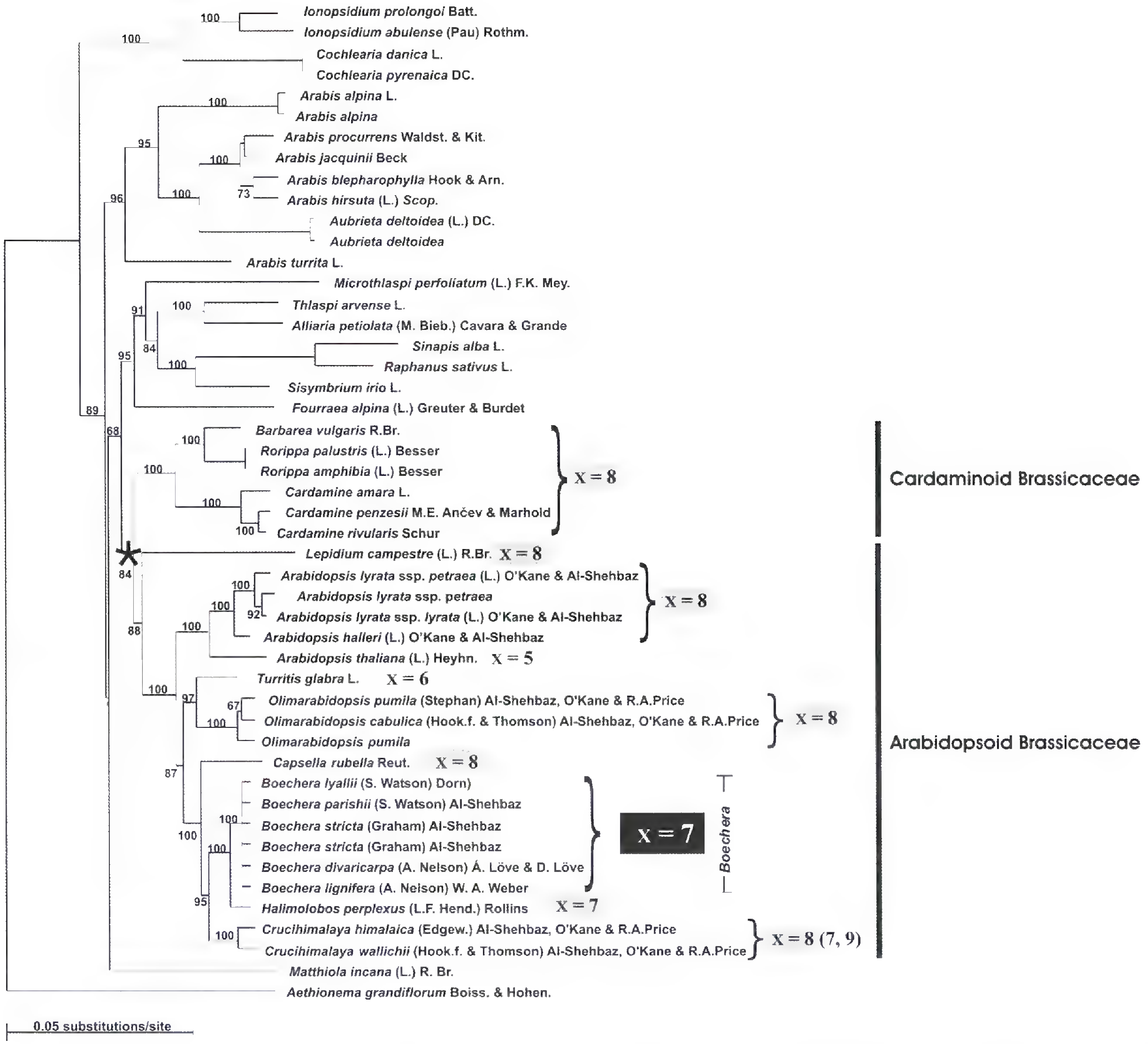

Figure 1. Phylogenetic relationships among cruciferous plants based on *chs* and *mat*K sequence data (redrawn from Koch et al., 2001, reprinted with permission from The Botanical Society of America). The asterisk marks the initiation of a *trn*F pseudogene tandem repeat at the basis of the cardaminoid and arabidopsoid Brassicaceae (Heenan et al., 2002; Koch et al., 2005). The phylogenetic distribution of chromosome numbers among the cardaminoid and arabidopsoid Brassicaceae is taken as evidence that the base chromosome number of the progenitor of these lineages was most likely $x = 8$.

Table 1a and 1b (pp. 520–524). Evidence for sexual and apomictic reproduction taken from karyological investigations, analyses of pollen, estimation of seed fertility, and population studies reported for *Boechera* species and affined taxa. Species names are according to Rollins (1993); taxonomic ranks are according to Mulligan (1996). Although most species are treated within genus *Boechera* (cf. Al-Shehbaz, 2003, for synonymy with *Arabis*), four *Arabis* species are also included. *Arabis petiolaris* and *A. serotina* probably have to be transferred to other genera (see below) but were included for clarity. The remaining two *Arabis* species have not yet been formally transferred to *Boechera*, but are included based on the similarity in genus cytology. Superscript index numbers refer to the publications listed in the footnote. Gray fields signify features associated with apomictic reproduction and species showing evidence of apomixis.

Table 1a

Taxon	Chromosome number[a]					Meiosis[c]		Type of Pollen[f]		Fertility		Population genetic studies[i]
	$2n = 14$	$2n = 14 \pm 2$	$2n = 21$	$2n = 21 \pm 2$[b]	others	Sex[d]	Apomeiosis[e]	Tetrads	Monads Dyads	% Pollen viability[g]	% Seed Set[h]	
Arabis boivinii[Y] G.A. Mulligan			2[4]				? M[4]					
Arabis depauperata[Y] A. Nelson & P.B. Kenn.	1[4]					M[4]						
Arabis petiolaris[X]					$2n = 28$[8]							
Arabis serotina[W]	1[20]											
B. breweri (S. Watson) Al-Shehbaz	1[7]									**90 ± 9[21]**	71 ± 29[21]	
B. canadensis (L.) Al-Shehbaz	1[10]											
B. cobrensis (M.E. Jones) Dorn	1[3]					P[3]						
B. constancei (Rollins) Al-Shehbaz	1[7]											
B. crandallii (B.L. Robinson) W.A. Weber	3[3.6]					P[3]						Iso - Sex[22]
B. demissa **(Greene) W.A. Weber**			1[6]									
B. divaricarpa	15	1, B: 1	9	4, B: 1	2	See Table 1b for details						
B. fendleri	7[3.6.19]					P[3], M[19]	P[3]					
			2[3.8]	1[8]			P[3]					
B. glaucovalvula (M.E. Jones) Al-Shehbaz	1[9]					P[9]						
B. gunnisoniana	1[3]					P[3]	E, P[40]					
			1[22]						D[22]	58[22]	38[22]	Iso - Apo[22]
B. holboellii	85	4, B: 5	28	4, B: 6	7	See Table 1b for details						
B. inyoensis **(Rollins) Al-Shehbaz**			1[7]	1[7]								
B. laevigata (Muhlenberg ex Willdenow) Al-Shehbaz	5[3.13.14.18.38]					P[3.14.18] M[13.38]						
B. lemmonii **(S. Watson) W.A. Weber**	3[6.10]											
			1[4]				? M[4]				abundant[4]	
B. lignifera	3[3.22]					P[3]		T[22]		**91[22]**	46[22]	Iso – Apo?[22]
B. lyallii			5[4.10.21]				? M[4], ? P[21]			34 ± 28[21]	65 ± 22[21]	
B. microphylla **(Nuttall) Dorn**	2[3.10]					P[3]						
	1[3]	1[29]					P[3,29]		D[29]			

Table 1a and 1b. Continued.

B. parishii	1[9]					P[9]						
B. pendulina (Greene) W.A. Weber	1[29]							uniform[29]				
B. perennans (S. Watson) W.A. Weber	2[3,7]					P[3,7]						
B. perstellata (E. Braun) Al-Shehbaz	2[6,15]					M[6,15]						
B. platysperma (A. Gray) Al-Shehbaz	1[21]					P[21]				**91 ± 11[21]**	77 ± 25[21]	
B. puberula (Nuttall) Dorn	1[4]		1[4]			M[4]	? M[4]					
B. pulchra (M.E. Jones ex S. Watson) W.A. Weber	3[7,9]		2[7]			P[9]						
B. repanda (S. Watson) Al-Shehbaz	1[3]					P[3]						
B. schistacea (Rollins) Dorn	1[29]							uniform[29]				
B. selbyi (Rydberg) W.A. Weber			1[8]									
B. shortii (*A. dentata*)	$2n = 12$[13]					M[13]						
B. sparsiflora (including Arabis columbiana)	9[2,4]	1[35]	3[4,7,21]	6[4,7,16,21,29] B: 1[7]	$2n = 46$ $2n = 32$[17]*	P[2],M[4]	? M[4] ?E[29], P[16,29] ? M[4]		M, D[29] Z	**88-97[2]** 62 ± 46[21]	73 ± 25[21]	
B. stricta	20		2	1	1	See Table 1b for details						
B. subpinnatifida (S. Watson) Al-Shehbaz	3[8,21,37]					P[8,37]				**95 ± 2[21]**	50 ± 16[21] 45 ± 18[21]	
B. williamsii (Rollins) Dorn												Mor–uniform[5]
B. crandallii x B. holboellii			1[6]									
B. divaricarpa x B. holboellii				2[28,29]			P[28,29]		D[29]			
B. holboellii x B. stricta			1[2]				? P[2]			19[2]		

Table 1a and 1b. Continued.

Table 1b

Taxon	Material denotation	Somatic Chromosome number	Meiosis[c]		Type of Pollen[f]		Fertility		Population genetic studies[i]	Citation[j]
			Sex[d]	Apomeiosis[e]	Tetrads	Monads Dyads	% Pollen viability[g]	% Seed Set[h]		
B. divaricarpa		[15] ("n = 15")		P						3
		16	P [?]							3
		14	M							4, 5; 11
		15; 21; 28		? M						4
		14; 22								6
		13 + 2B; 14; 20 + 2B; 21; 28								10, 31, 33
		21; 22		? P			64 ± 38	65 ± 19		21
B. holboellii	Colorado	21	E (0%--5%)	E (95%--100%),P			95			1
including	Greenland	14	E (11%--55%), P	E (45%--89%), P	Mixture of reduced and unreduced pollen		33			1
Arabis holboelli Hornemann	Greenland	21	E (2%--17%)	E (83%--98%)			50			1
A. collinsii Fernald	12 biotypes	14	P				92--99			2
A. exilis A. Nelson	2 biotypes	28; 28 + 1f	P				89--94			2
A. pendulocarpa A. Nelson		14	P, M							3, 17, 36
A. pinetorum Tidestr.		[14] ("n = 14")								3
A. retrofracta Graham		[21] ("n = 21")		P						3
		14	M (mostly)	? M (few)						4
		c. 21		? M		D				4
		21		? M; P						4, 29
		15	M	? M						4
		c. 22		? M						4

Table 1a and 1b. Continued.

	14							Mor–uniform	5; 6, 10, 28, 29, 30, 31, 32
	21								6, 10, 26, 28, 29
	21 ± 1								7
	14 (n = c.8 in a few cells)	P	? P						8
	13 + 2B								10
	20 + 2B								10
	14 + 1B, 14 + 1f								10, 12, 30
	14 (n = 7; 9)	P	? P			32 ± 18	72 ± 13		21
	28				D	85	46		22
	21 + 1f				D	(42)88--95	38--83.3	Mol – Apo[22,23]	22
	21				D	(3)73--97	(15)57--77		22
	14			T	D	86--92	32--51		22
HBH	21 + 1f		E, P	T	M, D				24, 25, 26
HBH	14	(E)	E		M, D				27
Disko 1	14								26, 27, 28
Disko 2	21		E, P						27, 28, 29
S. Str. 10	14	E, P	E, P	T	D, M				26, 27, 28
S. Str. 3	21		E, P	T	D, M				27, 28
S. Str. 9	21		E, P		D	Plant fertile, one completely sterile shoot			27, 28
Eqaluit	21		E, P		D				26, 27, 28
Alaska	14	E, P		T			Normal		26, 27, 28
No 3090	28								28
No 2820	35 (of accidental origin)								28
No 2820	2x		P		D				28

Table 1a and 1b. Continued.

	No 6	21 + 1f		P		D				29
	No 6	17					shrivelled			29
	No 12	14	M		T					29
	No 16	21 + 1B or 20 + 2B								29
	No 20, A-Batch	14; 14 + 1B; 16; 17			T	D				29
	No 20, B-Batch	21; 21 + 1B		M	T	D				29
		22								39
B. stricta		14	M, P				**98**			2, 4
(*A. drummondii*)		14	P							3, 8, 34
		21		? M						4
		14								5; 6, 10, 31
		20								10
		28	P		Reduced					29

[a] Number of published chromosome reports classified according to ploidy levels and the occurrence of additional chromosomes. Somatic triploidy was taken as evidence for apomictic reproduction. [b] B indicates that the additional chromosome(s) was a B chromosome. [c] E and P denote female or male gametogenesis, respectively; "M" signifies that the gender of the gametophyte has not been stated by the authors.* The count $2n = 32$ for *B. sparsiflora* was based on a misidentified true *Arabis* (M. Windham, pers. comm.) and, therefore, has not been considered in further statistics provided in the manuscript. [d] Cell division listed in this column showed characteristics indicative for sexual reproduction: complete, regular pairing of chromosomes at meiosis (bivalents); regular meiotic division resulting in gametes with reduced chromosome number. Crisscrossed fields underline that, so far, evidence for normal regular meiosis was not demonstrated in association with triploidy. [e] Divisions listed in this column showed characteristics indicative for apomictic reproduction: asyndesis, apomeiosis, gametophyte with unreduced chromosome number. A question mark (?) indicates irregular, often incomplete, pairing of chromosomes and irregular divisions, resulting in gametophytes with irregular chromosome numbers. [f] D, M, and T denote dyadic, monadic, and tetradic pollen. "Reduced" and "Unreduced" refer to chromosome number. [g] The percentage of stainable pollen grains is provided; estimates of fertility of pollen produced by sexuals are given in bold. [h] Values provided by Vorobik (1985) refer to fruit set, while those given in Roy (1995) are the percentage of germinating seeds. [i] Evidence for sexual ("Sex") and apomictic ("Apo") reproduction taken from population studies; "Iso" refers to population genetic studies using isozymes; "Mor" are observations on the variability of morphotypes. [j] Records of identical information content have been merged. [w] This species may belong to the genus *Pennellia* (Al-Shehbaz, pers. com.). [x] This species may belong to the genus *Streptanthus* (Al-Shehbaz, pers. com.; Koch & Dobeš, unpubl. data). [y] This species has formally not been transferred to *Boechera*. Therefore, it is nomenclaturally considered as an *Arabis*. [Z] Pollen was highly variable among flowers: (1) some flowers put out few dyads and monads, while the majority of pollen grains were of irregular size and shape; (2) some flowers formed dyad pollen only. Numbers in superscript

Table 1a and 1b. Continued.

refer to the following publications: 1 = (Naumova et al., 2001); 2 = (Johnson, 1970); 3 = (Rollins, 1941); 4 = (Mulligan, 1996); 5 = (Rollins, 1983); 6 = (Rollins, 1966); 7 = (Rollins & Rüdenberg, 1971); 8 = (Rollins & Rüdenberg, 1977); 9 = (Rollins & Rüdenberg, 1979); 10 = (Mulligan, 1964); 11 = (Taylor & Brockman, 1966); 12 = (Packer, 1964); 13 = (Smith, 1938); 14 = (Easterly, 1963); 15 = (Rollins, 1960); 16 = (Raven et al., 1965); 17 = (Taylor & Taylor, 1977); 18 = (Kovanda, 1978); 19 = (Ward, 1983); 20 = (Wieboldt, 1987); 21 = (Vorobik, 1985); 22 = (Roy, 1995); 23 = (Roy & Rieseberg, 1989); 24 = (Böcher, 1947); 25 = (Böcher, 1938); 26 = (Böcher & Larsen, 1950); 27 = (Böcher, 1951); 28 = (Böcher, 1954); 29 = (Böcher, 1969); 30 = (Sharbel et al., 2004); 31 = (Löve, 1982); 32 = (Löve, 1979); 33 = (Löve, 1975); 34 = (Löve, 1976); 35 = (Löve, 1969); 36 = (Dalgaard, 1988); 37 = (Stace, 1998); 38 = (Stace, 1989); 39 = (Stace, 1999); 40 = (Tsakin et al., 2004).

Böcher, 1969; Johnson, 1970; Rollins & Rüdenberg, 1971). Recent work has demonstrated these extra chromosomes to be B chromosomes (Camacho et al., 2000), as is evidenced by their interspecific origin, variable morphology, high content of heterochromatin, and independent evolution from the autosomes (Sharbel et al., 2004). Interestingly, the B chromosomes have a wide geographic distribution and can be found in both diploid and triploid *Boechera* (Sharbel et al., 2005). Furthermore, DNA sequence analyses of B chromosome alleles suggest a single origin for these elements (Sharbel et al., 2004).

However, chromosome number is the most intensively studied karyological property of *Boechera* that has been studied (Böcher, 1938; Smith, 1938; Rollins, 1941; Böcher, 1947; Böcher & Larsen, 1950; Böcher, 1951, 1954; Rollins, 1960; Easterly, 1963; Mulligan, 1964; Packer, 1964; Raven et al., 1965; Rollins, 1966; Taylor & Brockman, 1966; Böcher, 1969; Löve, 1969; Johnson, 1970; Rollins & Rüdenberg, 1971; Löve, 1975, 1976; Rollins & Rüdenberg, 1977; Taylor & Taylor, 1977; Kovanda, 1978; Rollins & Rüdenberg, 1979; Löve, 1979, 1982; Rollins, 1983; Ward, 1983; Vorobik, 1985; Wieboldt, 1987; Dalgaard, 1988; Stace, 1989; Roy & Rieseberg, 1989; Roy, 1995; Mulligan, 1996; Stace, 1998, 1999; Naumova et al., 2001; Sharbel et al., 2004; Tsakin et al., 2004), the data for which is now available for 36 species (34, if *Arabis petiolaris* and *A. serotina* E. S. Steele are excluded from the genus), comprising about half of the *Boechera* species recognized in the monography of Rollins (1993). Much of the current taxonomy in *Boechera* may be expected to be subject to far-reaching revision in the near future (Windham et al., 2004), but there is no doubt that $x = 7$ constitutes the common and probably only base chromosome number of the genus. The only taxon deviating from this rule may be *B. shortii* (Fernald) Al-Shehbaz (*A. dentata* Torr. & Gray), for which a single count of $n = 6$ II (bivalents) was published by Smith (1938). A total of 289 chromosome records (excluding counts reported repeatedly and for taxa probably belonging to other genera) are currently available. This total is strictly limited to those taxa currently recognized as *Boechera* s.s. (cf. Al-Shehbaz, 2003) and to direct observation of chromosome number rather than inference by flow cytometry or pollen size. In order to minimize propagation of any error in species recognition, we do not provide here the original data, which were collected in a taxonomic context. Instead, in addition to Table 1a and 1b, an annotated and fully documented database summarizing published data on karyology, pollen, and population genetics is available at <http://ephedra.hip.uni-heidelberg.de/brassicaceae>. (In both data files we applied the

taxonomy and nomenclature suggested in Rollins, 1993, Mulligan, 1996, and Al-Shehbaz, 2003, respectively.) These databases are continuously updated in regard to taxonomic identification. In addition, two databases that might be useful for additional information will be accessible in the future. A chromosome number database is compiling most references of chromosome counts in cruciferous plants (Warwick & Al-Shehbaz, 2006), and a crucifer taxonomy database is listing many new taxonomic treatments (Warwick et al., 2006). The most recent findings on *Boechera* are not considered in these databases, but updates will follow continuously.

From an evolutionary point of view, several obvious features with respect to chromosome numbers can be deduced from this overview. (1) Diploidy is very common, comprising 190 out of 289 chromosome records. (2) Polyploidy is primarily expressed on the triploid ploidy level ($2n = 3x$), although higher ploidy levels are also found in a limited number of reports ($N = 12$). (3) Aneuploid chromosomes occur frequently and are associated with both even and odd-ploids. (4) Provided that a sufficient number of counts were carried out, many of the individual taxa exhibited a variety of cytotypes, including diploids, polyploids, and aneuploids. However, it remains to be verified whether the latter feature represents a significant cytological pattern of differentiation or whether it merely reflects an erroneous assignment of accessions and artificial taxonomic classification of populations.

The unevenness in sampling must be considered, as 67% of the data (195 out of 289 records) describe the karyological differentiation in accessions attributable to three species only (*Boechera divaricarpa*, *B. holboellii*, and *B. stricta*), while 69% of the species so far investigated (25 out of 36) are represented by one to three chromosome counts only.

In addition, some of the karyological data require revision or reinterpretation, taking into consideration any ambiguities that may have resulted from varying degrees of synapsis and nonreduction in chromosome numbers during meiosis (Böcher, 1951; Johnson, 1970). As will be discussed in more detail in the next section ("Development of gametophytes"), the karyotypic irregularities common to *Boechera* embryogenesis and pollen development are associated with agamospermy and hybridization and may have resulted in several unreduced gametophytic chromosome numbers being published as haploid ones (Rollins, 1941), including *B. divaricarpa*, a count of $n = 15$; *B. fendleri* (S. Watson) W. A. Weber, 14 and 21; and *B. holboellii*, 14 and 21 (cf. comments in Böcher, 1969; Mulligan, 1996). Such high ploidy levels probably do not exist in *Boechera*. A true duplication of the somatic chromosome number within an individual has nonetheless been reported from the somatic tissues of *B. sparsiflora* (Nutt.) Dorn, $2n =$ ca. 23 and ca. $2n = 46$ (Böcher, 1969), the apparent outcome of an endomitotic event.

Aneuploidy has been reported (in terms of species numbers) eight times. However, it can be inferred from the observed pattern of cytological differentiation within *Boechera holboellii* that autosomal aneuploidy may be the exception rather than the rule. Thus only 9 somatic chromosome numbers out of the 139 records ascribed to this species were aneuploidies not attributable to B chromosomes. The infrequency of aneuploids may reflect the need for proper chromosome balance for pseudogamous endosperm formation in apomicts. In contrast, the flow cytometric data of Sharbel and Mitchell-Olds (2001) demonstrate high frequencies for aneuploid chromosomes of two size classes (cf. fig. 5 in Sharbel & Mitchell-Olds, 2001), the larger of which likely represents the autosomal aneuploid chromosome. This larger aneuploid chromosome was restricted to a single (or very few) chloroplast haplotype (Sharbel & Mitchell-Olds, 2001) and therefore may reach very high frequencies in specific geographic regions or genetic backgrounds. The smaller of the aneuploid elements is a B chromosome, which has a wide geographic distribution (Sharbel et al., 2005) and can be found in divergent genetic backgrounds (Sharbel et al., 2004), but has what appears to be a single origin based on B allele sequencing (Sharbel et al., 2004). This nonrandom distribution of Bs in apomictic individuals only, in conjunction with its wide distribution (i.e., evolutionary maintenance), implies that it either has a meiotic drive mechanism (cf. Camacho et al., 2000) or that it is somehow associated with apomictic reproduction.

While the *Boechera holboellii* genome frequently contains additional chromosomes (both B and aneuploid chromosomes), natural populations are typically composed of both diploid and triploid cytotypes (Roy, 1995; Sharbel et al., 2005). Recent cytological, palynological, and molecular research has provided us with the opportunity to describe and understand this pattern in more detail. Using pollen morphology and microsatellite allelic variation, Dobeš et al. (2004a) described diploidy and triploidy among 77 accessions of this species, whereas Sharbel and Mitchell-Olds (2001) and Sharbel et al. (2005) demonstrated the occurrence of B chromosomes in both of these cytotypes using flow-cytometry and karyology. These results are concordant with those collected from light microscopical investigation of chromosomes. For example, Naumova et al. (2001) carried out chromosome counts on 37 plants from

Colorado and Greenland representing eight separate seed batches and one bulked seed collection but found exclusively euploid diploids and euploid triploids. Because no tetraploid individuals have been identified in these mixed populations, it is hypothesized that environmental effects (e.g., cold shock) may trigger the production of unreduced gametes, which eventually contribute to triploid zygote formation (Sharbel & Mitchell-Olds, 2001; Sharbel et al., 2005). The frequent and repeated generation of triploid cytotypes within natural populations and in different genetic backgrounds (Sharbel & Mitchell-Olds, 2001; Sharbel et al., 2005) provides further evidence that unreduced gamete production is common in this genus (cf. Böcher, 1951). Triploids were demonstrated to be of allopolyploid origin (Sharbel et al.. 2004; Dobeš et al., 2004a), and in this case it is unclear how genome dosage and subsequent phenotypic effects differ between independently derived triploid lineages (Sharbel et al., 2005). Autopolyploidy was suggested based on the frequent sharing of haplotypes between diploids and triploids (Sharbel & Mitchell-Olds, 2001). It was further shown that certain diploid and triploid cytotypes share identical to genetically highly similar nuclear ribosomal ITS sequence types (Dobeš et al., 2004a). However, based on microsatellite allelic variation, polyploid individuals always were found to show some extent of heterozygosity (Dobeš et al., 2004a). Therefore, we have so far no strict evidence for autopolyploidy in *Boechera*, neither on the genotypic nor on the species level. It may be speculated, then, that polyploidization can only be triggered in diploid hybrids via the formation of unreduced gametes (see discussion below). It is furthermore unknown whether reported ploidy levels higher than $3x$ are the result of similar phenomena (i.e., zygote formation from unreduced gametes in mixed populations of *B. holboellii*) or if these cytotypes are of a different evolutionary history. Although based on much smaller datasets, cytological characteristics similar to those in *B. holboellii* are also exhibited by several other *Boechera* species (cf. Table 1a and 1b; <http://ephedra.hip.uni-heidelberg.de/brassicaceae>).

A second type of cytological differentiation with respect to chromosome numbers was encountered in several species so far observed to be represented by euploid diploids only. We mention here explicitly two examples. First, *Boechera stricta*, which is also a good example to discuss possible limits of morphology-based species recognition in *Boechera*. The majority of chromosome counts identified this species as a diploid one. However, triploids were also found among the investigated accessions (Sharbel & Mitchell-Olds, 2001; Sharbel et al., 2005). Subsequent morphological investigations (Windham & Al-Shehbaz, unpublished data) have shown that the triploids identified as *B. stricta* have actually undergone hybridization with another species. Support for these hypotheses was recently found using microsatellite allelic markers (cf. Dobeš et al., 2004a). Another conspicuous example is represented by a certain morphotype of *B. holboellii*, *B. holboellii* var. *retrofracta* (= *B. retrofracta* (Graham) Á. Löve & D. Löve). A significant proportion of diploid specimens assigned to this variety showed covariation of characteristic plastid and nuclear sequence polymorphisms (Dobeš et al., 2004a). These genotypes were interpreted to constitute a basal evolutionary unit within a highly polymorphic and taxonomically artificial *B. holboellii*. These examples demonstrate that karyologically heterogenous species may actually be an amalgamation of different taxa, at least some of which can be characterized by single chromosome numbers and a restricted number of genotypes, respectively.

Finally, based on our recent evaluation of data, we may define a third type of karyological differentiation represented by taxa that so far proved to comprise triploids only. Solely triploid taxa seem to be extremely rare according to current taxonomic classification of *Boechera*. Nevertheless, future taxonomic concepts can integrate knowledge on values of apomictic reproduction of triploids or the age of apomictic clones, which may ultimately lead to the recognition of cytologically more uniform species.

Development of Gametophytes

Our cytological knowledge on the development of embryosacs and male gametogenesis in *Boechera* comes mainly from the work of Tyge W. Böcher (Böcher, 1951, 1954, 1969) and contributions by Naumova et al. (2001) and Tsakin et al. (2004). Apomictic *Boechera* are diplosporous (the embryo develops from an unreduced embryosac mother cell) similar to the *Taraxacum* L.-type, and it appears that pseudogamy is maintained given that fertilized endosperm has been identified in both diploids and triploids (Böcher, 1947, 1951; Naumova et al., 2001; Tsakin et al., 2004). Based mostly on pollen analyses, sexuality has been shown to be associated with complete chromosome bivalent formation at meiosis, followed by regular heterotypic and homotypic divisions, to produce gametes with reduced chromosome numbers while pollen was tetradic and usually of high viability (Böcher, 1951). In contrast, apomictic gametogenesis involved either complete asyndesis or irregular pairing of chromosomes during meiosis I, followed by the formation of a restitution nucleus to

result in gametes with unreduced chromosome numbers (Böcher, 1951). Pollen was either of the dyadic or monadic type. Apomeiotic development was often accompanied by pathways exhibiting approximately normal meiosis with varying numbers of univalents, resulting in tetrad pollen with varying chromosome numbers and relatively low fertility (Böcher, 1951; Sharbel et al., 2005). Although these latter developmental traits can be considered to be associated with apomixis, the occurrence of meiotic abnormalities probably cannot be equated with apomictic reproduction itself.

Complete analyses of embryological developmental stages have been performed from a limited number of accessions of *Boechera holboellii* or infraspecific members of this complex (Rollins, 1993) originating from Greenland ("Disko"; "Botanical Garden of Copenhagen"; "Eqaluit"; the Sondre Strømfjord) and two localities in the western United States (Colorado; Washington state) (Böcher, 1951, 1969; Naumova et al., 2001). In addition to these studies, Tsakin et al. (2004) analyzed the embryology of one accession from Colorado identified as *B. gunnisoniana* (Rollins) W. A. Weber. Any other indications of apomixis were obtained from karyological investigations of isolated stages of female gametogenesis, population genetic studies (Rollins, 1983; Roy, 1995), observations on reproductive biology (Johnson, 1970; Vorobik, 1985; Roy, 1995), and analysis of pollen formation (e.g., Böcher, 1951; Dobeš et al., 2004a). Therefore, embryological studies have so far been performed on two species, *B. holboellii* s.l. and aff. *B. gunnisoniana*, from a few geographic areas only.

From these considerations we can estimate the importance and frequency of the particular reproductive modes in *Boechera*. We have summarized published data on karyology, pollen and seed formation, fertility, and within-population differentiation in Table 1a and 1b and in the supplementary database (available on request and at <http://ephedra.hip.uni-heidelberg.de/brassicaceae>). Important traits that enable the differentiation of apomixis and sexuality, including pollen formation, degree of chromosome pairing at meiosis, and chromosomal reduction, also were considered, although nuclei showing irregular chromosome pairing at meiosis may not necessarily be indicative of apomeiosis. Given this uncertainty, these irregular pairing constellations were not considered sufficient to judge the reproductive mode of a given individual. Furthermore, we used the argument that stable triploidy should be associated with apomixis (cf. Sharbel & Mitchell-Olds, 2001), because no known sexual pathway in *Boechera* could explain the maintenance of uneven ploidy levels. As *Boechera* are annuals, biennials, and short-lived perennials without any effective modes of vegetative propagation, agamospermy seems to be the only possible mechanism through which triploidy can be inherited. However, triploidy does not necessarily mean obligate apomixis, and these cytotypes can potentially give rise to offspring of different ploidy levels.

Although apomixis is a female trait (i.e., asexual reproduction through egg cells), it can be inferred from observations of pollen formation because apomeiosis is reflected in both the male and female components of *Boechera* (Böcher, 1951). For example, Böcher (1951: 33) demonstrated correspondence between the modes of male and female gametogenesis in several accessions ("Disko 2," "HBH 3x," "S.Str. 3," sterile shoot in "S.Str. 9," and "S.Str. 10"). This correlation was even observed in specific inflorescences in facultative apomictic *Boechera* (i.e., those producing seed both through sex and apomixis). For instance, a high degree of chromosome pairing during female meiosis was identified in flowers from the same inflorescence in which highly synaptic meiosis was identified in pollen mother cells ("HBH 3x" and "S.Str. 10" material) (Böcher, 1951). Furthermore, high degrees of syndesis were correlated with seed sterility and decreased pollen viability on a particular branch of the inflorescence in the triploid "S.Str. 9" accession (Böcher, 1951).

Taking the above-mentioned traits into consideration, we were able to find evidence of apomictic reproduction in accessions assigned to 17 species. Apomixis was associated with (1) diploidy, triploidy, or rarely tetraploidy; (2) aneuploidy and euploidy; (3) formation of dyadic and monadic pollen or tetradic pollen of usually low viability; and (4) low levels of genetic or morphologic differentiation within population. Apomixis is rarely the only mode of reproduction in any *Boechera* species, and hence nine of the 17 species for which apomixis was identified are likely amphi-apomictic complexes (cf. Table 1a and 1b), which presumably have to be split into separate taxonomic entities. However, amphi-apomictic lineages have to be expected given the report of decreased values of apospory in *Boechera* (cf. Naumova et al., 2001 and discussion below).

Despite the accumulated amount of chiefly descriptive data regarding reproduction in *Boechera*, we still have poor knowledge of the genetics and inheritance of apomixis in this genus. A first approach to infer the genetic basis of apomixis was recently made by Sharbel et al. (2004), who hypothesized that the B chromosomes may somehow be associated with the expression of the apomictic trait. Considering that the B chromosome in geographically and genetically distinct apomictic lineages is composed of a contigu-

ous genomic region, Sharbel et al. (2004) proposed that it is evolutionarily important because it has not been lost by genetic drift, as would be expected for a neutral or deleterious B chromosome (Camacho et al., 2000). However, cases of apomeiotic formation of gametophytes in the absence of extra chromosomes have been reported (Rollins, 1941; Böcher, 1951, 1954), and thus Sharbel et al. (2004) argued that such an apomixis factor could also be expected to be present in autosomes. It should be noted that several experts in *Boechera* taxonomy have some doubt on some counts provided by Rollins (1941).

The gathered data (e.g., Johnson, 1970; Rollins, 1941; Mulligan, 1996; Rollins & Rüdenberg, 1977, 1979) provided evidence for the existence of sexual species that were mostly diploid, exhibited complete chromosome pairing and meiotic chromosomal reduction, and were characterized by high pollen viability and seed fertility. These taxa (e.g., *Boechera stricta*) are characterized by euploid and diploid chromosome numbers and produce *Polygonum* L. –type embryosacs via the meiotic pathway (Naumova et al., 2001; Tsakin et al., 2004). Recent taxonomic studies estimate the actual number of sexual diploid *Boechera* to be at least 70 (Al-Shehbaz & Windham, pers. comm.). Evidence for what is possibly purely sexual reproduction in polyploids has been provided for three accessions only (*B. holboellii*, $2n = 28$; $28 + 1f$, Johnson, 1970; *B. stricta*, $2n = 28$, Böcher, 1969). In contrast, and as expected from theoretical considerations, the reduction of chromosome numbers associated with regular bivalent formation was rarely observed in triploids.

Interestingly, syndesis in *Boechera* is not only genotypically determined, i.e. reflecting homology of chromosomes, but it also can be modificative. Böcher (1951) explained the facultative occurrence of syndesis to be controlled by an unknown physiologic factor. This is best shown by the fact that apomeiosis and meiotic pairing can occur side by side and in definite parts within a single inflorescence (Böcher, 1951; Naumova et al., 2001). Additionally, changes in temperature or environmentally induced differences in rate of growth of plants were shown to make *B. holboellii* change from apomeiotic to meiotic development, or at least change from fertility to sterility. Therefore, the available data indicate that we can expect various reproductive pathways to co-occur frequently among plants of a population and even within single individuals.

Pollen Formation

Male gametogenesis has been favored over the study of the development of female gametophytes by several authors (e.g., Rollins, 1941; Easterly, 1963; Raven et al., 1965; Johnson, 1970; Vorobik, 1985), because pollen is easily and abundantly available. Pollen viability can routinely be inferred from simple staining procedures (Vorobik, 1985; Naumova et al., 2001), pollen grain shape and size (Böcher, 1951; Roy, 1995; Dobeš et al., 2004a; Sharbel et al., 2005), and germination experiments (Böcher, 1951). Furthermore, correlations between the size of pollen grains and their DNA content have repeatedly been shown in several other genera (Ehrendorfer, 1949; Stepánková, 1993; Trávnícek & Vinter, 1999; Vilhar et al., 2002; Lihová & Marhold, 2003), and thus relative pollen ploidy can also be estimated.

Apomictic *Boechera* is a highly interesting and promising system to study pollen cytology, as gametes with highly variable chromosome numbers can be produced by single individuals (Böcher, 1951, 1969). For example, tetradic, dyadic, and monadic pollen have been observed within specific parts of a single inflorescence, with monad pollen mainly observed in the lowermost portion of the inflorescence, while dyads prevailed in its middle part (Böcher, 1951, 1969). Both types of pollen resulted from apomeiotic gamete development, which was often followed by the formation of a restitution or contraction nucleus. In any of these apomeiotic pathways, one (heterotypic division; formation of dyads) or both (heterotypic and homotypic division; monads) of the divisions corresponding to those in normal meiosis were abandoned (cf. Böcher, 1951: 21 seq.). As a consequence, gametes can be produced with either unreduced chromosome numbers or with double the somatic chromosome number of their bearers, as has been shown in somatic triploids that produce both triploid and hexaploid pollen (e.g., Böcher, 1951; Kravtchenko et al., 2001). Double pollen grains possessing four generative and two vegetative nuclei have also been observed (Böcher, 1951).

In contrast, the formation of tetradic pollen generally involved some degree of chromosome pairing followed by a reductional division. Gametes produced via this pathway by individuals exhibiting evidence for apomixis were reported to contain highly variable chromosome numbers, the result of cytological irregularities during their formation (cf. Böcher, 1951, 1969). Gametes containing chromosome numbers that deviated from those expected under a scenario of either regular meiotic division or complete (apomeiotic) nonreduction have been observed by several authors (Rollins, 1941; Böcher, 1951; Johnson, 1970; Vorobik, 1985).

A conspicuous case was described by Böcher (1969), who identified two different classes of synaptic (i.e., syndetic) triploids based on pollen size data and

chromosome configurations during meiosis I, including those that produced only large pollen and those that produced a bimodal distribution of smaller pollen size. Those triploids producing a single class of relatively large pollen often showed regular metaphase I with 10 bivalents plus one univalent, rather than the seven trivalents or corresponding lower numbers of bivalents and univalents (Böcher, 1951). Such pairing formations have subsequently been observed by several authors (Böcher, 1951, 1969; Johnson, 1970) and have recently been supported by pollen analyses (Sharbel et al., 2005). Regular bivalent formation in triploids was hypothesized to be the outcome of structural chromosome mutations (Böcher, 1951), although it is difficult to understand how such mutations (a random process) could convergently lead to a similar pattern of synapsis in different triploid lineages (Sharbel & Mitchell-Olds, in prep.). Although these cytological irregularities led to a considerable decrease in pollen viability (Böcher, 1951; Vorobik, 1985), a limited number of gametes were still fertile and capable of participating in the production of viable offspring (Böcher, 1969; see later discussion).

Nogler (1984) suggested that alleles responsible for apomixis may act as, or are linked to, recessive lethal factors, as would be expected in an asexual organism (Kondrashov, 1985). The accumulation of recessive lethal mutations in apomicts over time would therefore lead to decreasing fertility of haploid gametes. Indeed, Naumova et al. (2001) observed a mixture of reduced and unreduced pollen grains in apomictic diploid *Boechera holboellii*, while only unreduced female and male gametes contributed to mature seed. These results suggested, as stated by these authors, that there was selection against haploid gametes. Alternatively, proper dosage of an apomixis factor may be important, and haploid gametes may simply be unable to express this trait. However, tetradic pollen produced by sexuals was usually of high quality (Johnson, 1970; Vorobik, 1985; Roy, 1995) and obviously was formed by normal and undisturbed meiosis.

Data on the chromosomal composition of male gametes have recently been supplemented with morphological analyses of pollen. Although the size of pollen grains appeared highly variable among species (Vorobik, 1985; Roy, 1995) and within individuals (Böcher, 1951), Dobeš et al. (2004a) demonstrated that pollen size can be used to identify diploid sexuals in *Boechera holboellii* and *B. stricta*. Furthermore, plants capable of apomictic reproduction were characterized by a multimodal distribution of pollen sizes (Böcher, 1951). These various classes of pollen size corresponded to tetradic, dyadic, and monadic pollen, respectively, as well as to two distinct sizes of pollen mother cells. Böcher (1951) concluded that formation of pollen with unreduced chromosome number is frequent in apomictic *B. holboellii*, taking place in some diploids and all triploids. This observation is also in agreement with the results of Roy (1995), Naumova et al. (2001), and Kravtchenko et al. (2001), who also found formation of dyads as well as of monads to be common.

Establishment of Offspring

Two main reproductive pathways allowing the stable and constant inheritance of chromosome number in specific cytotypes have been identified in *Boechera*: regular meiosis in euploid diploids and tetraploids and agamospermy in a variety of cytotypes. Sexual *Boechera* appear to be highly self-compatible and hence inbreeding is very common, as has been inferred through isozyme patterns (Roy, 1995) and microsatellites (Dobeš et al., 2004a). The floral biological investigations of Johnson (1970) on nine biotypes assigned to *B. holboellii* and *B. lyallii* (S. Watson) Dorn, *B. sparsiflora*, and *B. stricta* demonstrated that each was self-pollinating and was adapted for some outcrossing by insects (cf. Rollins, 1971). Johnson (1970) also identified different biotypes co-occurring at single sites and discovered evidence for mechanical and ethological (i.e., preference of different insects to certain biotypes) isolation mechanisms between them. Although the above observations provide clear evidence for strong isolation between lineages, repeated introgression between sexual taxa and also between sexuals and apomictics is likely frequent at both the intra- and interspecific levels (Koch et al., 2003; Sharbel et al., 2004; Dobeš et al., 2004a, 2006). Thus, hybrids between *Boechera* species have been repeatedly obtained in crossing experiments (Johnson, 1970; Vorobik, 1985; Roy, 1995) and observed in the field (e.g., Rollins, 1983, 1993; Mulligan, 1996). At present, the importance of hybrid speciation in the radiation and diversification of the genus is widely accepted (Windham et al., 2004). While hybridization in *Boechera* was previously thought and demonstrated to be associated with polyploidization and the apomictic stabilization of new genotypes (Böcher, 1951; Sharbel & Mitchell-Olds, 2001; Koch et al., 2003; Dobeš et al., 2004a), the report of diploid and sexual *B. divaricarpa*, a hybrid between *B. holboellii* (and probably other species) and *B. stricta*, may provide evidence that homoploid sexual hybrids have played a similarly important role as polyploidization in the establishment of new species.

As with regular meiosis, apomixis potentially allows for the stable inheritance of chromosome number in

the course of reproduction. Furthermore, agamospermy resembles autogamy, a special case of sexual reproduction often encountered in *Boechera* that leads to offspring having the same genotype as their parent (Roy, 1995). However, a fundamental difference between agamospermy and apomixis is that apomixis maintains heterozygosity and stabilizes polyploid, aneuploid, and hybrid genomes. The population genetic consequences of apomictic reproduction include the coexistence of different and potentially crossable but clearly distinct morphotypes within populations (Rollins, 1983), in addition to low intrapopulation level differentiation (Roy, 1995; Naumova et al., 2001). Whereas agamospermy in *Boechera* is almost never obligate, facultative apomixis has frequently been demonstrated (Böcher, 1951, 1969; Naumova et al., 2001), with average values for apomeiosis during female gametophyte development ranging from 73% to 98% in *B. holboellii* (Naumova et al., 2001). Naumova et al. (2001) also observed apomictic embryos with somatic ploidy levels double that of their mothers, the result of fusion between unreduced male and female gametes and therefore deviating from normal parthenogenetic development. The above-mentioned mechanisms, in addition to variable chromosomal synapsis (Böcher, 1951, 1969), imply that apomixis plays a significant and specific role in the establishment of new genotypes. Additional genetic variation can be expected from crossing-over events between chromosomes (i.e., automixis) at various pairings, which were reported to take place even in apomictic plants (Böcher, 1951, 1969).

The role of apomeiotic development of gametes in the origin of triploids, which represent the most common ploidy level in *Boechera*, is particularly well understood. Böcher (1951) previously pointed out that amphi-apomictic diploids could easily produce triploid offspring by fusion of reduced and unreduced gametes. The frequent and repeated establishment of triploid genotypes within and among various evolutionary lineages has been confirmed by Sharbel and Mitchell-Olds (2001) and Sharbel et al. (2005) through the use of chloroplast sequence variation. Dobeš et al. (2004a) and Sharbel et al. (2004) have furthermore established that these polyploid cytotypes are the outcome of crossing events between similar to largely diverged genotypes. By analogy, agamospermous diploids might pass the apomictic trait without a change in ploidy levels to genetically recombined offspring when occasional fusion of two reduced gametes takes place, and this may occur between two apomicts or even between an apomict and a sexual individual. However, the establishment of triploids may have also involved diploid pollen from tetraploids. Although somatic tetraploids were found to be extremely rare in *Boechera*, they may be evolutionarily significant. Thus Verduijn et al. (2004) demonstrated that tetraploid dandelions (genus *Taraxacum* L., Asteraceae) give rise to mainly triploid offspring in crosses with diploid sexuals. A similar scenario may apply to *Boechera*, as was recently hypothesized by Dobeš et al. (2004a). Unlike *Taraxacum*, in which tetraploids are the only cytotype putting out diploid pollen with high frequency, unreduced gamete production appears to be relatively common among diploid *Boechera*.

While the origin of triploids can be explained by the above processes, the establishment of diploid apomicts is much less obvious. However, an intriguing possibility is that triploids that produce bimodal pollen sizes (i.e., pollen with 14 + B or a complement of 7 chromosomes) may be the source of apomictic diploid 2C + B *Boechera holboellii* (Böcher, 1969; Sharbel et al., 2005). This explanation would allow shifts between diploids and triploids and facilitate regular genetic exchange between these cytotypes (cf. Verduijn et al., 2005).

Evidence for exemplary hybrid origin in *Boechera* is provided and discussed in Dobeš et al. (2006). The origin of diploid and triploid cytotypes, both of which are the most frequently encountered in *Boechera*, is concordant with the chromosomal composition of gametes. However, the scarcity of tetraploids and higher ploidy levels in natural populations suggests that natural selection acts against their formation, with genomic balance or stabilization through apomixis. We can say so because it appears that selection does not have a significant impact on gametes, considering that dyad and monad pollen were shown to have morphological integrity (Dobeš et al., 2004a) and high viability (Böcher, 1951; Roy, 1995). Furthermore, unreduced pollen was shown to successfully fertilize the central cell of embryosacs, which is required for pseudogamous endosperm development (Naumova et al., 2001; Tsakin et al., 2004).

Conclusions

We can expect that the processes described above would lead to a large variety of new genotypes and cytotypes with distinct chromosome numbers. Furthermore, these new types may potentially become fixed through asexual reproduction, as meiotic irregularities were chiefly observed in individuals carrying the apomictic trait. However, the reproductive success of such genetically recombinant and genomically heterogeneous progenies has never been demonstrated in the long term, and their evolutionary significance is not fully understood yet. It will be

a promising field of future experimental research to correlate structural changes of the genome in hybrid offspring with fitness measures over several generations, which we presumably can do as soon as linkage maps become available (cf. Rieseberg et al., 2000). Estimation of the performance of hybrid genotypes and cytotypes will enable us to assess whether hybrids are merely byproducts of evolution or whether they themselves actively drive diversification in this genus.

The North American *Boechera* group is a highly complex species aggregate within Brassicaceae. However, the group itself is clearly defined and restricted to North America, which is also true for most of its close relatives. For this reason, it is realistic that the ongoing projects focusing on its taxonomy, systematics, evolutionary history, and phylogeography will provide a good framework to understand speciation and evolution in this notoriously difficult group. Additional research on molecular mechanisms of apomixis, genome structure, and chromosomal synteny and collinearity will provide data that bridge evidences from cytology and embryology to species diversity.

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A SYSTEMATIC STUDY OF THE OLD WORLD GENUS *FOCKEA* (APOCYNACEAE–ASCLEPIADOIDEAE)[1,2]

P. V. Bruyns[3] *and C. Klak*[3]

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Abstract

The six species of *Fockea* Endl. (Apocynaceae, Asclepiadoideae, Fockeeae) occur in Africa south of the equator from southern Kenya to South Africa. A phylogeny for all six species of *Fockea* is inferred from data obtained from two chloroplast markers (the *trn*L-F region and the *psb*A-*trn*H intergenic spacer), one nuclear marker (ITS1 region), and morphology. *Fockea* is found to be monophyletic and sister to the bitypic *Cibirhiza* Bruyns. Morphologically, *Fockea* is characterized by the deeply tubular outer corona that is filled by the erect, inflated sterile appendages of the anthers. Of the six species, the widely distributed but exclusively tropical *Fockea multiflora* K. Schum. is sister to the other five members of *Fockea*, and, among these five, the widely distributed and mainly tropical *F. angustifolia* K. Schum. is sister to the remaining four, which are endemic to southern Africa. It is shown that *Fockea* most probably originated in South Tropical Africa. A complete taxonomic account is provided for the six species of *Fockea*, and their known distribution is mapped. Lectotypes are designated for *Fockea capensis* Endl., *F. monroi* S. Moore, *F. schinzii* N. E. Br., *F. sessiliflora* Schltr., and *F. sinuata* (E. Mey.) Druce. Neotypes are designated for *Brachystelma macrorrhizum* E. Mey., *Fockea angustifolia*, and *F. comaru* (E. Mey.) N. E. Br. An isotype has been located for *F. multiflora*.
Key words: Apocynaceae, Asclepiadoideae, *Fockea*, ITS1 region, morphology, phylogeny, *psb*A-*trn*H intergenic spacer, southern Africa, taxonomy, *trn*L-F region.

The small genus *Fockea* Endl. is endemic to Africa south of the equator. It was established in 1838 by Stephan L. Endlicher for the single species, *F. capensis* Endl. He based the description of this species on a specimen cultivated at Schönbrunn Garden in Vienna (here lectotypified by *Schönbrunn Garden 488* (K, W)), which previously had been given the illegitimate name *Cynanchum crispum* Jacq. (*non C. crispum* Thunberg, 1794). This famous specimen cultivated at Schönbrunn Garden under the number 488 was collected in the Cape Colony after 1786 by Franz Boos and Georg Scholl. It was still in cultivation in Vienna in 1930 (Marloth, 1932) and, until about that time, was reputed to be the only surviving member of the species. This myth was exploded by Rudolf Marloth, who collected *F. capensis* near Prince Albert in South Africa. The plant collected by Boos and Scholl remains alive in Vienna to this day (Zecher, 1988).

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The first recorded gathering of *Fockea* was made during the expedition of Simon van der Stel of 1685–1686 to the Copper Mountains of Namaqualand in South Africa. Material was found north of Clanwilliam between the Olifants River and the Doorn River and was figured in an unpublished manuscript by Jan Commelin. This figure was later identified as *F. edulis* (Thunb.) K. Schum. (Wijnands et al., 1996). However, *F. edulis* does not occur anywhere near Clanwilliam, and this plant was *F. comaru* (E. Mey.) N. E. Br. An early collection of *F. edulis* was made by C. P. Thunberg near the Gouritz River in southern South Africa in October 1772. He described this as *Pergularia edulis* Thunb. in 1794 and later placed it in the genus *Echites* P. Br. Early gatherings of the small and inconspicuous species *F. comaru* and *F. sinuata* (E. Mey.) Druce were made by Johann Franz Drège, probably between 1832 and 1833. Ernst H. F. Meyer, who worked on Drège's collections, does not seem to have been quite sure what to do with these two species and described them both as possible members of *Brachystelma* Sims (Meyer, 1838). Only after 1900 did they come to be associated with *Fockea*.

Both widely distributed and mainly tropical species, *F. angustifolia* K. Schum. and *F. multiflora* K. Schum. were described rather later by Karl Schumann (Schumann, 1893). *F. angustifolia* has by far the most extensive synonymy of any species of *Fockea*, probably because of its wide distribution and the variability in the shape of the leaves and the size of the flowers.

A further genus involving species of *Fockea*, *Chymocormus* Harv., was established by William H. Harvey (1842). He based this on *Zeyher 965* (K), which he considered to represent Thunberg's *Pergularia edulis*, with a "corona so remarkable, that I do not hesitate to propose it as the type of a new genus" (1842: 24). However, although Harvey did mention "*Pergularia ? edulis*, Thunb. (*Zeyher, 965*)" (1842: 24) as belonging to *Chymocormus*, he made no valid new combinations (Greuter et al., 2000: ICBN Art. 33.1) and published no new names in *Chymocormus*.

Modern taxonomic investigations into *Fockea* began with an informal account by M. B. Bayer, where the various species were discussed and several previously unknown facts were brought to light (Bayer, 1976). This account was based on material at the Karoo Garden, Worcester, South Africa. A revision was prepared by Court (1982) for a Master's degree at Rhodes University, South Africa. Morphological features were investigated in this account for their taxonomic relevance and it was found that, whereas the flowers were useful for characterizing the genus, only features of the leaves could be used to distinguish the species. Five species (*F. comaru*, *F. crispa* K. Schum., *F. edulis*, *F. multiflora*, and *F. sinuata*) were recognized, but this account was never published. A summary of some of the results of Court (1982) appeared in the popular journal *Asklepios* (Court, 1987), where six species (*F. angustifolia*, *F. comaru*, *F. crispa*, *F. edulis*, *F. multiflora*, and *F. sinuata*) were discussed. This differed from the account of 1982 in that *F. angustifolia* and *F. comaru* were treated as separate species.

N. E. Brown (1902–1903: 427) mentioned that *Fockea* "appears to form a connecting link between the tribes *Secamoneae* and *Marsdenieae*," but he placed it in the Marsdenieae because the pollinia lacked a differentiated margin and are horizontal in the anther thecas (Brown, 1902–1903; 1907–1909). Kunze (1993) pointed out that many peculiar features of this genus suggested a more "basal" position in the Asclepiadoideae. Later a new tribe, Fockeeae, was published for the two genera *Fockea* and *Cibirhiza* Bruyns (Kunze et al., 1994). This tribe was said to be distinguished from the Marsdenieae and others by the shared derived characters of the complex corona, the large anther appendages, and certain characters of the translator, namely the absence of true caudicles, the attachment of the pollinia on the side of the corpuscle closest to the style head, and the lack of a floor in the corpuscle connecting its flanks.

In fact, many of these characters do not distinguish the Fockeeae from other asclepiads. A complex corona is also found in *Eustegia* R. Br., where the ontogeny has been found to follow a similar pattern to that of *Fockea* (Bruyns, 1999: 25, fig. 4). The corona of *Sarcostemma viminale* (L.) R. Br. is also of complex construction (for its ontogeny see Endress & Bruyns, 2000: 26, fig. 11). At 2–3 mm long, the appendages of the anthers are unusually large in all species of *Fockea*, but in both species of *Cibirhiza* they are less than 0.5 mm long (e.g., Kunze et al., 1994: 370, fig. 4). Certainly they are larger (at 1 mm long) in many species of *Microloma* R. Br. (e.g., Bruyns & Linder, 1991: 505, fig. 17) than they are in either species of *Cibirhiza*. Furthermore, the appendages in *Telosma africana* (N. E. Br.) N. E. Br. resemble those in *Fockea* in that they are longer than the fertile part of the anther and have somewhat inflated margins. As Kunze (1993) showed, the pollinarium of *Fockea* exhibits many features of species of *Secamone* R. Br., and one of these is the lack of true caudicles, with the pollinia attached in both cases to a dorsal process of the corpuscle. Verhoeven et al. (2003) found that the wall of the pollinia and the pollen grains differed markedly in *Fockea* and *Cibirhiza*: in *Cibirhiza* the wall is present and the grains are single (as in the Asclepiadoideae), while in *Fockea* the wall is absent and the grains are in tetrads (as in the Secamonoi-

Table 1. Vouchers for *Fockea* and other Apocynaceae used in molecular analyses with Genbank accession numbers for nuclear (ITS1) and chloroplast (*psb*A-*trn*H, *trn*L-F) gene regions.

Accession	Origin	ITS1	*psb*A-*trn*H	*trn*L-F
Cibirhiza albersiana	Tanzania, near Gulwe, *Bruyns 9652a* (BOL)	AM233381	AM231756	AM233363
Cibirhiza dhofarensis	Oman, Dhofar, *Miller 7525* (E, K)	AM233382	AM231757	AM233364
Fockea angustifolia, acc. 1	Namibia, Van Zyl's Pass, *Bruyns 8054* (BOL)	AM233385	AM231760	AM233367
Fockea angustifolia, acc. 2	South Africa, Muden, *Bruyns 9406a* (BOL)	AM233384	AM231759	AM233366
Fockea angustifolia, acc. 3	Tanzania, near Kondoa, *Bruyns 9632* (E)	AM233386	AM231761	AM233368
Fockea angustifolia, acc. 4	Zambia, Sinazongwe, *Bruyns 9587* (MO)	AM233383	AM231758	AM233365
Fockea capensis	South Africa, Plathuis, *Bruyns 7340* (NBG)	AM233387	AM231762	AM233369
Fockea comaru, acc. 1	Namibia, Numeis, *Bruyns 8821* (MO)	AM233388	AM231763	AM233370
Fockea comaru, acc. 2	South Africa, near Port Elizabeth, *Dold 2381* (GRA)	AM233389	AM231764	AM233371
Fockea edulis	South Africa, near Steytlerville, *Bruyns 7051* (BOL)	AM233390	AM231765	AM233372
Fockea multiflora, acc. 1	Namibia, Okonguati, *Bruyns 4089* (NBG)	AM233391	AM231766	AM233373
Fockea multiflora, acc. 2	Tanzania, near Gulwe, *Bruyns 9651* (E)	AM233392	AM231767	AM233374
Fockea multiflora, acc. 3	Zambia, N of Monza, *Bruyns 9593* (MO)	AM233393	AM231768	AM233375
Fockea sinuata	Namibia, near Maltahöhe, *Bruyns 5670* (MO, WIND)	AM233394	AM231769	AM233376
Raphionacme monteiroae	Tanzania, near Gulwe, *Bruyns 9652* (K)	AM233395	AM231770	AM233377
Rhyssolobium dumosum	South Africa, Alexander Bay, *Bruyns 3948* (BOL)	AM233396	AM231771	AM233378
Secamone filiformis	South Africa, Grahamstown, *Bruyns 8990* (E)	AM233397	AM231772	AM233379
Telosma africana	South Africa, Empangeni, *Bruyns 9340* (BOL)	—	AM231773	AM233380

deae). However, they still considered that the "presence of a gynostegial corona fused into an undulate annulus around the base of the gynostegium, in addition to a staminal corona of free segments" (Verhoeven et al., 2003: 70) was one distinguishing feature of the Fockeeae. This is despite a similar construction being present in *Sarcostemma viminale* and the fact that the corona in *Fockea* does not form an "undulate annulus around the base of the gynostegium" but is a tubular structure that exceeds the length of both the anthers and the style head and dominates the gynostegium.

The morphological position is therefore quite confused. Consequently the Fockeeae was abandoned in Endress and Bruyns (2000), and the two genera were again referred to the Marsdenieae.

Molecular results (Sennblad, 1997; Civeyrel & Rowe, 2001; Potgieter & Albert, 2001; Verhoeven et al., 2003) suggested that at least some members of *Fockea* and *Cibirhiza* are sisters to the remainder of the Asclepiadoideae. Sennblad (1997) found that, according to *rbc*L data, *F. tugelensis* N. E. Br. was nested within the Periplocoideae and *C. albersiana* H. Kunze, Liede & Meve was sister to the Asclepiadoideae. However the specimen (*Sennblad 237*) that had been determined by U. Meve as *F. tugelensis* was later found to be *Petopentia natalensis* (Schltr.) Bullock of the Periplocoideae (Sennblad, 1997, note added in proof) and the specimen (*Specks 248*) identified as *C. albersiana* was *Fockea multiflora* (Verhoeven et al., 2003) so that, according to *rbc*L data *F. multiflora* is sister to the Asclepiadoideae. Civeyrel & Rowe (2001) found the same position for *F. capensis* with *mat*K data. Using *trn*L-F data, Potgieter & Albert (2001) found that *F. cylindrica* R. A. Dyer, *F. edulis*, and *F. sinuata* were sister to the Asclepiadoideae. However, the credibility of these results is again called into question by the misidentification of material, since these authors found distinct positions on their cladogram for *Stapelia revoluta* Masson and *Tromotriche revoluta* (Masson) Haw., although the former is the basionym of the latter! Using data from one chloroplast gene region, Verhoeven et al. (2003) showed that *Cibirhiza dhofarensis* Bruyns, *Fockea edulis*, and *F. multiflora* formed a monophyletic group that is sister to the remainder of the Asclepiadoideae.

We build on the results of Verhoeven et al. (2003). Using both molecular and morphological data, we show that the two species of *Cibirhiza* and all six species of *Fockea* belong to a monophyletic tribe, the Fockeeae, and we elucidate the relationships among the species of *Fockea*. We give a detailed account of all species of *Fockea*, paying particular attention to the three widespread and variable species, *F. angustifolia*, *F. comaru*, and *F. multiflora*. Information on the distribution of the species has been much extended since Court (1982), and these data are included.

Materials and Methods

Material from the herbaria BM, BOL, COI, GRA, K, KMG, LISC, M, NBG, NU, P, PRE, S, SAM, WIND, and Z was examined. Vouchers used for the molecular analyses are listed in Table 1. Table 2 provides the scoring for the morphological character states.

Table 2. Character states (0, 1) for the 13 morphological characters (1–13) (see App. 1 for definitions) used in the cladistic analyses. A dash indicates that the character is not applicable and the question mark that the state is unassignable.

	Morphological characters		
	00000	00000	111
Species	12345	67890	123
Cibirhiza albersiana	11001	10111	010
Cibirhiza dhofarensis	11001	10111	010
Fockea angustifolia, acc. 1	11001	00110	000
Fockea angustifolia, acc. 2	11001	00110	000
Fockea angustifolia, acc. 3	11001	00110	000
Fockea angustifolia, acc. 4	11001	00110	000
Fockea capensis	10100	10110	000
Fockea comaru, acc. 1	11001	00110	000
Fockea comaru, acc. 2	11001	00110	000
Fockea edulis	1010?	10110	000
Fockea multiflora, acc. 1	0--01	10110	000
Fockea multiflora, acc. 2	0--01	10110	000
Fockea multiflora, acc. 3	0--01	10110	000
Fockea sinuata	11000	00110	000
Raphionacme monteiroae	11001	110--	-1-
Rhyssolobium dumosum	0--11	000--	-11
Secamone filiformis	0--01	0110-	110
Telosma africana	0--11	1010-	101

Illustrations were made from living material in some cases and in others from material preserved in alcohol.

INGROUP AND OUTGROUP SAMPLING

Raphionacme monteiroae (Oliv.) N. E. Br., *Rhyssolobium dumosum* E. Mey., *Secamone filiformis* (L. f.) J. H. Ross, and *Telosma africana* were taken as outgroups (Civeyrel & Rowe, 2001; Verhoeven et al., 2003), with *R. dumosum* and *T. africana* chosen from the Marsdenieae, where the Fockeeae had previously been placed. *Secamone filiformis* was chosen as a representative of the Secamonoideae, while *Raphionacme monteiroae*, from the Periplocoideae, was used to root the tree (Verhoeven et al., 2003). We treated the eight species (12 accessions) of the Fockeeae as our ingroup. Representatives of all six species of *Fockea* were used, and several accessions were included for the widespread species *F. angustifolia*, *F. comaru*, and *F. multiflora*. Both species of *Cibirhiza*, *C. dhofarensis* and *C. albersiana*, were incorporated. In total, 18 accessions were included in the *trn*L-F and *psb*A-*trn*H data-sets. There were 17 accessions in the ITS1 data-set, which excluded *Telosma* because a sequence could not be obtained. For vouchers and Genbank accession numbers, see Table 1.

DNA EXTRACTION AND AMPLIFICATION OF TEMPLATE DNA

Total DNA was isolated from fresh leaf material of the 18 samples by the method of Saghai-Maroof et al. (1984) as modified by Doyle and Doyle (1987). The three DNA regions were amplified from total DNA by polymerase chain reaction (PCR). The *trn*L-F region (consisting of the adjacent *trn*L intron and *trn*L-F intergenic spacer) was amplified using primers c and f (Taberlet et al., 1991). The *psb*A-*trn*H intergenic spacer was amplified using primers *psb*AF and *trn*HR (Sang et al., 1997). The ITS region was amplified using primers ITS2 (Baldwin, 1992) and 18KRC (5′-GCACGCGCGC-TACACTGA-3′). Twenty-five microliter reactions were prepared, which contained 19 μL of sterile water, 2.5 μL of 10× PCR buffer, 1 μL of 10 mmol/L dNTPs in equimolar ratio, 0.75 μL of each 10 μmol/L primer, 0.5 μL of 25 mmol/L $MgCl_2$, 0.125 μL of Taq DNA polymerase (5 U/μL), and 0.5 μL of genomic DNA. In general, a 10× dilution of the extraction product was used as template DNA. Thermal reactions were carried out as follows: first 2 min. at 97°C, initial denaturation, 1 cycle; denaturing at 95°C for 1 min.; annealing at 52°C for 45 sec.; extension at 72°C for 2 min.; the three cycles repeated 30 times, and finally followed by extension for 8 min. at 72°C. The reactions were cleaned using the QIAquick PCR purification kit from Qiagen and the purified products were eluted in 60 μL of sterile water.

SEQUENCING AND ALIGNMENTS

Both strands of the PCR products were cycle sequenced, using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, California, U.S.A.). The primers used for amplification were also used for the sequencing reactions. The samples were run on an Applied Biosystems 377 automated DNA sequencer.

Data files were assembled and edited using GeneDoc version 2.6.002 (Nicholas & Nicholas, 1997) and Chromas version 1.43 (McCarthy, 1996–1997). Sequences were aligned by eye. Ambiguous positions were coded using appropriate IUPAC ambiguity symbols so as to maximize retention of information. The method of simple indel coding of Simmons and Ochoterena (2000) is followed, in which all gaps were treated as single sites, coded as binary characters and added to the data matrix. Areas of ambiguity in the alignment were excluded from all analyses.

Table 3. Taxa used in the analysis of ancestral areas and their presence (1) or absence (0) in six regions: (1) Cape Region; (2) Succulent Karoo Region; (3) Nama Karoo Region; (4) Tropical and subtropical Southern Africa; (5) South Tropical Africa; and (6) Arabia.

	Region					
Species	1	2	3	4	5	6
Secamone filiformis	0	0	0	1	1	0
Cibirhiza albersiana	0	0	0	0	1	0
Cibirhiza dhofarensis	0	0	0	0	0	1
Fockea angustifolia	0	0	1	1	1	0
Fockea capensis	1	1	0	0	0	0
Fockea comaru	1	1	1	0	0	0
Fockea edulis	1	0	0	1	0	0
Fockea multiflora	0	0	0	1	1	0
Fockea sinuata	0	1	1	0	0	0

CLADISTIC ANALYSES

Three matrices were analyzed, one consisting of combined *trn*L-F and *psb*A-*trn*H sequences for all 18 accessions and a second of ITS1 sequences for 17 accessions (excluding *Telosma*). Due to the uniparental mode of inheritance of the plastid genome, we would not expect incongruent patterns of relationships from the different plastid regions, and so we analyzed only the combined matrices for the *trn*L-F and *psb*A-*trn*H data. A third matrix consisted of combined *trn*L-F, ITS1, and *psb*A-*trn*H spacer sequences for all 18 accessions (*Telosma* coded as "?"). No tests of congruence were performed before combining the data, because incongruent nodes were at most weakly supported (Jackknife support percentage, JK, < 63).

All cladistic analyses were performed using the parsimony algorithm of PAUP* version 4.0b4 (Swofford, 2000). Each data matrix was analyzed using 1000 replicates of random taxon-addition to find local minima in the tree-space, TBR (tree bisection-reconnection) branch swapping with MULPARS on, and all character transformations treated as equally likely (Fitch, 1971). At most two trees were saved on each replicate to minimize time spent swapping at local minima in the tree-space. All trees found in the initial 1000 replicates were then used as starting trees for a second round of TBR swapping with a tree limit of 30,000. To assess clade support, the data were analyzed using the jackknife option as implemented in PAUP*. It is known that, with a removal probability of 36.79%, JK 63 or more corresponds to a node supported by at least one uncontradicted character and may be regarded as supported by the data (Farris et al., 1996; Backlund & Bremer, 1997; Bakker et al., 1998). Therefore, the percentage of deleted characters for all jackknife analyses in this study was fixed at 36.79%. Only groups with JK greater than 50 were retained.

The ancestral area method of Bremer (1992) was used to locate the geographic origin of *Fockea*. The analysis was performed using PAUP*, with *Secamone filiformis* and the two species of *Cibirhiza* as outgroups. The area over which the species occur was divided into six regions: (1) Cape Region, (2) Succulent Karoo Region, (3) Nama Karoo Region, (4) Tropical and subtropical Southern Africa, (5) South Tropical Africa, and (6) Arabia. The occurrence of the species in these areas is given in Table 3.

RESULTS

Statistics, including numbers of variable positions and measures of consistency, are given for each analysis in Table 4.

CHLOROPLAST *trn*L-F AND *psb*A-*trn*H ANALYSIS

The strict consensus (Fig. 1) of the four trees recovered shows a monophyletic *Fockea* (JK 52), which is sister to the two species of *Cibirhiza* (JK 78). Within *Fockea*, three clades are retrieved and these form a polytomy with *F. sinuata* and the two accessions of *F. comaru*. The three clades are: (1) the four accessions of *F. angustifolia* (JK 98), (2) the three specimens of *F. multiflora* (JK 99), and (3) *F. capensis* and *F. edulis* (JK 63).

NUCLEAR (ITS1) ANALYSIS

The strict consensus (Fig. 2) of the four trees recovered shows a highly supported monophyletic *Fockea* (JK 98), which is sister (JK 100) to *Cibirhiza*. The nuclear data achieved a higher resolution among the species of *Fockea* than the chloroplast data. Within *Fockea*, the three accessions of *F. multiflora* form a monophyletic clade (JK 96), which is sister to the remainder of *Fockea* (JK 70). The remaining taxa fall into a polytomy consisting of two major clades, *F. edulis* and *F. capensis*. The two major clades are: (1) all four accessions of *F. angustifolia* (JK 71) and (2) *F. sinuata* and the two accessions of *F. comaru* (JK 75).

COMBINED MOLECULAR ANALYSIS

As in the previous analysis, the strict consensus of the two trees recovered (not shown) shows a well-supported, monophyletic *Fockea* (JK 90), which is sister to *Cibirhiza*. With both nuclear and chloroplast data, the relationships within *Fockea* are well resolved and mostly well supported. The three accessions of *F.*

Table 4. Statistics for cladistic analyses and trees for *Fockea* and related taxa. CI, Consistency index; RI, retention index; RC, rescaled consistency index.

Data partition	Total characters	Variable characters	Informative characters	No. of shortest trees	Tree length	CI	RI	RC	Indels
*trn*L-F	864	41	26	—	—	—	—	—	2
*psb*A-*trn*H	401	36	77	—	—	—	—	—	8
Chloroplast	1265	77	103	4	165	0.752	0.823	0.619	10
ITS1	637	113	69	4	134	0.761	0.799	0.608	3
All molecules	1902	190	172	2	309	0.731	0.788	0.576	13
Molecules and morphology	1915	203	185	4	327	0.722	0.781	0.563	13

multiflora are again sister (JK 82) to the remaining species of *Fockea*. The remainder forms a well-supported clade (JK 100) consisting of the four accessions of *F. angustifolia*, which is sister to a weakly supported clade (JK 53) made up of two main clades. These two clades are (1) *F. capensis* and *F. edulis* (JK 83) and (2) *F. sinuata* and the two accessions of *F. comaru* (JK 70). The two accessions of *F. comaru* are not sister taxa, since one of them is sister to *F. sinuata*. However, this relationship gained only minimal support (JK 52) and may therefore be spurious.

We show one of the two equally parsimonious trees as a phylogram (Fig. 3). The relatively long branches at the bases of the various accessions of *F. angustifolia* and *F. multiflora* show that the two tropical species are well separated from each other and from the remaining four species of *Fockea*, which have accumulated far fewer molecular changes. There are also numerous molecular changes among the four accessions of *F. angustifolia*. Similarly, in the other widespread species, *F. multiflora*, there are several molecular changes. In contrast, among the more local *F. comaru* and *F. sinuata* there is only one molecular change, which places one accession of *F. comaru* (*PVB 8821*) as sister to *F. sinuata*. These two, in turn, are sister to the second accession of *F. comaru* (*Dold 2381*).

COMBINED MORPHOLOGY AND MOLECULAR ANALYSIS

Here data for all 18 accessions were analyzed, including the 13 morphological characters listed in Appendix 1. In the strict consensus (not shown) of the four trees recovered. *Cibirhiza* and *Fockea* are monophyletic and sister to one another (JK 95 & 88, respectively). *Fockea multiflora* remains sister to the rest of *Fockea*, which forms a strongly supported clade (JK 85). Less resolution is achieved among the other species of *Fockea*, with the weakly supported southern clade (*F. comaru* and *F. sinuata*) of Figure 3 collapsing to a polytomy with *F. angustifolia*.

BIOGEOGRAPHY

Results of the ancestral area analysis (Table 5) show that the highest ratio of gain to loss occurs in the South Tropical Africa region (Area 5), followed by Tropical and subtropical Southern Africa (Area 4). The lowest ratios are in the Succulent Karoo Region (Area 2) and in Arabia (Area 6). A higher gain to loss ratio for a given area indicates a higher probability that this area is ancestral.

Discussion

1. MONOPHYLY OF *FOCKEA*

In all of our analyses *Fockea* is monophyletic and sister to a monophyletic *Cibirhiza*. Although the monophyly of *Fockea* is poorly supported in our chloroplast analysis (JK 52, Fig. 1), both the nuclear (JK 98, Fig. 2) and the combined molecular analyses (JK 90, Fig. 3) show high support for the monophyly of *Fockea*. The long branch subtending the *Fockea* clade, shown in Figure 3, indicates that *Fockea* is well separated from its sister *Cibirhiza*. Morphologically the two genera are well separated too. *Fockea* is characterized by the tubular outer corona enclosing the anthers and much exceeding them, with the inner lobes partially fused to the inside of this tube, and the erect, swollen appendages of the anthers that more or less completely fill the corona tube and much exceed the style head. *Cibirhiza* is characterized by a low outer corona ring surrounding the whole gynostegium, with a tooth behind each slender and terete inner lobe. The anther appendages are short and adpressed to the style head.

2. RELATIONSHIPS AMONG THE SPECIES OF *FOCKEA*

Fockea consists of two widespread, mainly tropical species (*F. angustifolia* and *F. multiflora*) found from Kenya to Namibia and South Africa and four much more local taxa (*F. capensis*, *F. comaru*, *F. edulis*, and

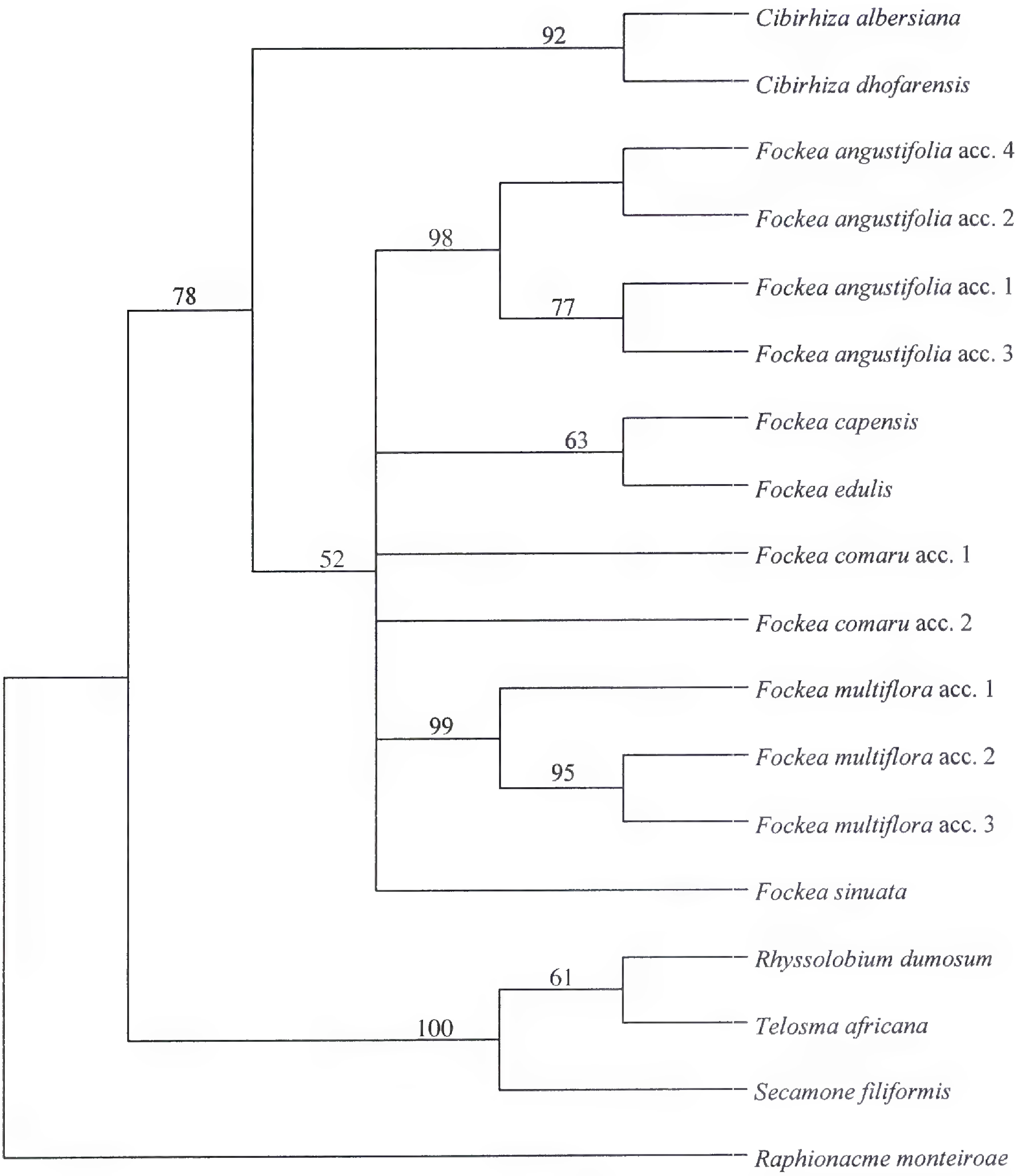

Figure 1. Strict consensus of four trees obtained from analysis of combined data from the two chloroplast genes *trn*L-F and *psb*A-*trn*H. Numbers above branches indicate jackknife support percentages.

F. sinuata) that are endemic to Namibia and South Africa. The starkest morphological contrast within the genus is beween *F. multiflora*, which is a massive, tropical liane without a tuber, and the others, which are relatively small climbers with a swollen, mostly subterranean tuber.

Relationships within *Fockea* are well resolved and mostly well supported. In addition, the relationships suggested by the molecular results are frequently congruent with those from the morphological characters. *F. multiflora* is sister to the rest of *Fockea*. Among the tuberous species, the mostly tropical *F. angustifolia*, is, in turn, sister to the remaining taxa that are endemic to southern Africa. Among the southern African taxa, *F. capensis* and *F. edulis* are well supported sisters and both have large, slightly exposed tubers, substantial stems, and elliptic to nearly circular leaves. Relationships among the small species having slender stems and mainly linear leaves are more complex, with the two southern African taxa

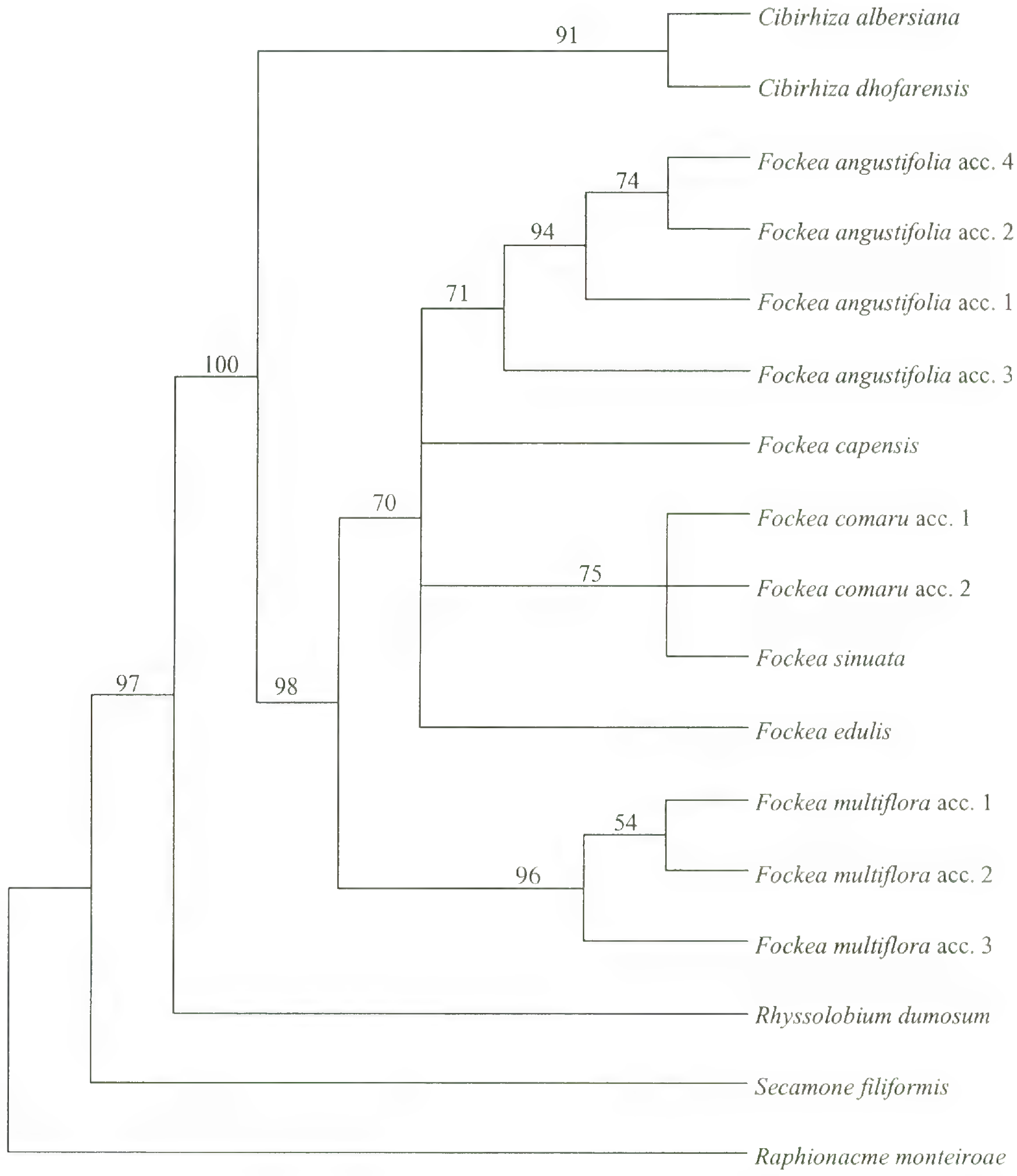

Figure 2. Strict consensus of four trees obtained from analysis of nuclear ITS1 data. Numbers above branches indicate jackknife support percentages.

(*F. comaru* and *F. sinuata*) grouping together but *F. angustifolia* remaining well outside this grouping. This is particularly interesting as *F. angustifolia* and *F. comaru* may occur together and are morphologically very similar.

The phylogram (Fig. 3) shows that both of the widespread, mainly tropical species, *F. angustifolia* and *F. multiflora*, lie on comparatively long branches, while the more local southern African endemics lie on shorter branches. This corroborates studies in other families, where extensive radiation in southern Africa has been accompanied by relatively small changes in the gene regions examined (e.g., Klak et al., 2003; 2004). As in *Fockea*, radiation in these other families is especially associated with the arid winter rainfall zone and its margins. In addition, considerable

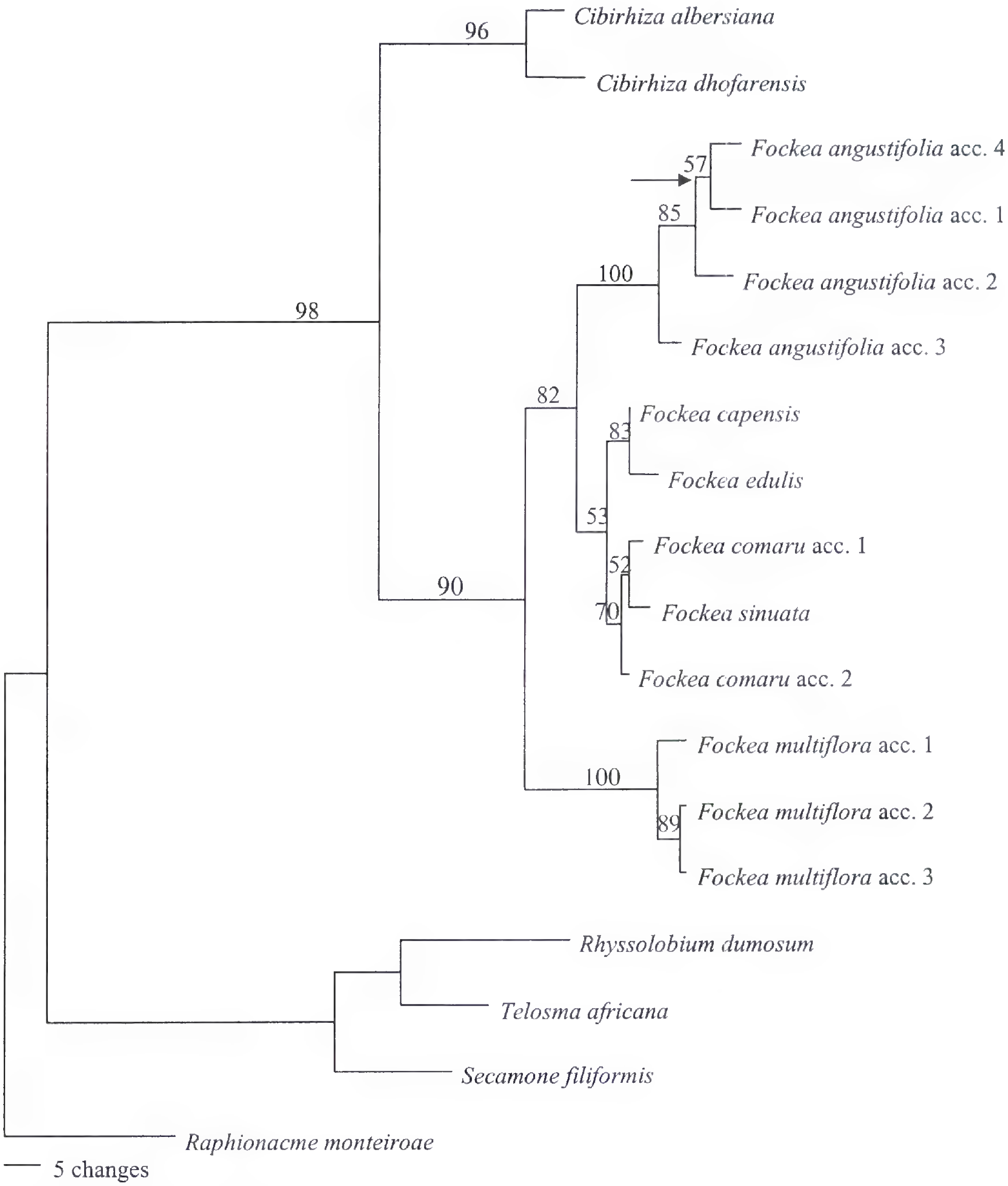

Figure 3. Phylogram of one of two trees obtained from combined analysis of chloroplast *trn*L-F, *psb*A-*trn*H, and nuclear ITS1 data. The lengths of the branches are in proportion to the number of changes in the nucleotides. The arrow indicates a node that collapses in the strict consensus tree. Numbers above branches indicate jackknife support percentages.

molecular variation is found among the different accessions of each of the widespread, mainly tropical species of *Fockea*. In fact, the phylogram shows that these accessions vary more among each other than do all the accessions in the southern clade, where relatively few molecular changes have occurred. It is possible that these tropical species of *Fockea* are much more ancient than the southern taxa.

3. RELATIONSHIPS WITHIN SPECIES IN *FOCKEA*

Our sampling contained multiple accessions of three of the most variable and widespread species.

We included three accessions of *Fockea multiflora*. In each of the molecular analyses, they formed a clade that is strongly supported. In the combined chloroplast analysis (Fig. 1) and the combined molecular

Table 5. The number of *Fockea* species gained and lost for each of six geographic areas. The proportion of gains/losses was used in the ancestral area analysis (Bremer, 1992) to determine the geographic origin of *Fockea*.

	Gains	Losses	Gains/Losses
Area 1: Cape Region	3	5	0.6
Area 2: Succulent Karoo Region	2	5	0.4
Area 3: Nama Karoo Region	2	4	0.5
Area 4: Tropical and subtropical Southern Africa	4	3	1.3
Area 5: South Tropical Africa	4	2	2.0
Area 6: Arabia	1	3	0.3

analysis (Fig. 3), the southernmost collection is sister to the others.

We included four accessions of *Fockea angustifolia* and found that they consistently formed a clade that is strongly supported in the combined chloroplast analysis (Fig. 1) and in the combined molecular analysis (Fig. 3), though less so in the ITS1 analysis (Fig. 2). In the combined molecular analysis (Fig. 3), the northernmost accession (*Bruyns 9632*) is sister to the others, which form a strongly supported clade relative to it. The wide morphological variation known in *F. angustifolia* in southern Africa and the lack of any significant morphological differences between these northern collections and those further south make the recognition of separate taxa here impossible, despite the strong support for clades within *F. angustifolia*.

We included two accessions of *Fockea comaru*. In the combined molecular analysis (Fig. 3), one accession of *F. comaru* (*Dold 2381*) comes out as sister to a clade consisting of *F. comaru* and *F. sinuata*. Figure 3 shows that this is caused by a difference in a single amino acid, which is also reflected in the weak support for the *F. comaru–F. sinuata* clade (JK 52).

4. BIOGEOGRAPHY AND ECOLOGY

Our ancestral area analysis suggests that *Fockea* originated in South Tropical Africa and radiated southward. *Fockea* is endemic to Africa south of the equator, and most species are found in southern Africa. Only two species (*F. angustifolia* and *F. multiflora*) extend north of this. Both of these reach Tanzania and are the most widely distributed members of the genus. *Fockea angustifolia* is the most widely distributed of all and is recorded from the subtropical Kimberley and Prieska area of central South Africa (in and to the east of the Nama Karoo Region of Jürgens, 1991) to southern Kenya. *Fockea multiflora*, on the other hand, is a purely tropical species occurring in northern Namibia and southern Angola, the basins of the Okavango and Zambezi Rivers, and in central Tanzania. The distributions of both *F. angustifolia* (Fig. 5) and *F. multiflora* (Fig. 9) exhibit a marked disjunction between the valley of the Zambezi River and central Tanzania. These patterns coincide largely with the more arid woodland or scrub of *Acacia* Mill., *Commiphora* Jacq., and *Balanites* Delile (where they are found) and the more mesic woodland dominated by *Brachystegia* Benth., where they tend not to occur.

The remaining four species are endemic to the semi-arid to arid, temperate to subtropical parts of South Africa and Namibia. *Fockea capensis* is the most restricted, occurring on the Little Karoo and in some of the drier surrounding mountains in southern South Africa in the Succulent Karoo Region (Jürgens, 1991). *Fockea edulis* is mainly found in semi-arid patches in the coastal parts of southern and southeastern South Africa from the Succulent Karoo Region eastward. *Fockea comaru* and *F. sinuata* are more widely distributed in South Africa and Namibia. *Fockea comaru* is strongly (but not exclusively) associated with the western part of South Africa, receiving winter rainfall, and is particularly found in the Succulent Karoo Region. Its distribution extends into the Nama Karoo Region (Jürgens, 1991) of central South Africa. *Fockea sinuata* is mainly found within the Nama Karoo and on the eastern margins of the Succulent Karoo Region. The shorter branches subtending these four species suggest that this radiation may have been more recent than the radiation within *F. angustifolia* and *F. multiflora*, where the branches are mostly longer.

Fockea angustifolia, *F. comaru*, and *F. sinuata* all occur close together in some areas on the Great Karoo of South Africa but, whereas *F. angustifolia* and *F. comaru* may actually grow in the same habitat, *F. sinuata* occupies a distinct niche in which *F. angustifolia* is rarely found and where *F. comaru* never grows. *Fockea comaru* occurs together with *F. edulis* on the Worcester-Robertson Karoo (southwestern South Africa) and very occasionally with *F. capensis* on the Little Karoo of southern South Africa.

Most species of *Fockea* occur on rocky hills, where the edible tubers are wedged tightly among stones and

protected from excavation. *Fockea angustifolia* occasionally grows in flat, pan-like areas, and *F. sinuata* is almost exclusively found in calcareous, pan-like areas, which become seasonally but very intermittently moist. All species, except *F. multiflora*, have a geophytic tendency, often with the ability to die back to the tuber under very dry conditions.

5. POLLINATION

Two facts suggest that the method of pollination in *Fockea* is not the same as in most other asclepiads. Firstly, the flowers are remarkable for the extremely restricted access to the pollinaria, and, unusually, the main organs causing these restrictions are the anther appendages, which block the corona tube. Between adjacent inner corona lobes there are three narrow channels leading to the base of the corona. Two of these are on the sides of the long outer corona lobules, and a fine hair inserted down either of these is directed exactly to the base of the corpuscle. The other channel lies behind the lowest part of the outer corona, and it provides access to the nectarial orifice below the corpuscle. Secondly, the margins of the anthers are schlerenchymatous only for a very small distance near their base or are not hardened at all. The schlerenchymatous part is found below the corpuscle but does not continue below it for some distance, as is customary.

In field-collected flowers, it has been found in *Fockea* that very few pollinaria are removed from their position on the style head. The only germinating pollinia have been found in the base of the longer channels reaching the nectarial orifices, and it appears that pollination is achieved if pollinia are deposited sufficiently far down these channels. The rudimentary guide-rails appear to direct a probing proboscis toward the base of the corpuscle. This enables the pollinarium to be removed, but the guide-rails seem to play no role in the deposition of the pollinia. It seems that the weak corpuscle partly breaks up and in so doing probably causes the pollinium to be wiped off the pollinator's proboscis in the narrower parts of the channels (the guide-rails may assist in wiping them off too). Evidence suggests that the same mechanism is involved in *Cibirhiza* (Kunze et al., 1994).

Pollination in the Periplocoideae is achieved when pollen is wiped off the spoon-like receptacle of the translator onto the base of the style head (Bruyns & Klak, pers. obs.). Here guide-rails are altogether absent. In the Secamonoideae, guide-rails are present and they guide potential pollinators toward the corpuscle for removal, but it is unknown what role they play in the deposition of pollen. In the Fockeeae, rudimentary guide-rails are present and they guide potential pollinators toward the corpuscle for removal, but they appear to play no role in the deposition of pollen. These three groups are successive sisters to the rest of the Asclepiadoideae, in which the guide-rails are better developed. In the rest of the Asclepiadoideae, the guide-rails assist in the removal of the pollinarium but have the unique additional function of holding the inserted pollinium as the pollen tubes grow.

TAXONOMY

Fockea Endl., in Endl. & Fenzl, Nov. Stirp. Dec. 3: 17. 1839. TYPE: *Fockea capensis* Endl.

Chymocormus Harv., London J. Bot. 1: 23–24 (1842). TYPE: Uitenhage, *Zeyher 965* (K!).

Erect to twining herb to massive liane often with underground to slightly exposed tuber tapering into small taproot anchoring plant, with fibrous roots, sap milky. *Stems* dextrorsely twining or erect, 80 mm–15 m long, 2–300 mm thick, slightly fleshy, finely pubescent when young, later covered with a shiny gray bark. *Leaves* opposite, spreading, subcoriaceous, gray-green to green, pubescent (with fine verrucose hairs) to glabrous; *petiole* 0–25(–45) mm long, spreading; *blade* 13–60(–150) × 1.5–20(–100) mm, linear to elliptic, acute to obtuse, apiculate, margins slightly to strongly revolute, non-succulent, deciduous, midrib paler than rest. *Inflorescences* extra-axillary, 1- to 20-flowered, umbellate, pubescent; *peduncle* 0–15 mm long, stout, with several short bracts at bases of pedicels; *pedicels* 1–15 mm long. *Sepals* adpressed to corolla tube, lanceolate, acute, 1.5–3 × 1 mm, pubescent outside and glabrous inside; *corolla* rotate, 8–22(–40) mm diam.; outside pubescent, gray-green; inside puberulous to glabrous, green to brown; *tube* 1.5–5 mm long, ca. 2 mm broad at mouth, ± glabrous within; *lobes* (3–)5–12(–18) × ca. 2 mm, linear, obtuse, spreading, usually spiralling to left, often twisted to left when viewed along lobe; *corona* consisting of 2 series of lobes, white, glabrous; outer forming cylindical tube with several series of erect to spreading lobules arising at mouth of tube; inner consisting of 5 erect lobules partly fused to outer corona tube lower down and usually pressed to backs of anther appendages and exceeding them; *anthers* consisting of erect ± quadrangular fertile part pressed to style head, above this with much inflated erect, transparent-white sterile appendage 2–3 mm long, these appendages connivent and pressed to one another, filling up area inside corona tube; *style head* less than 2 mm long, not exceeding fertile part of anthers, slightly bifid at truncate apex, below this widening to base of anthers then narrowing and sessile

on ovaries; *pollinarium* with 2 small translucent nearly flat and elliptical erect pollinia sessile on small brownish usually narrowly elliptical corpuscle. *Follicles* 50–220 × 8–30 mm, pendulous, broadly fusiform and narrowing into slender beak, uniformly glaucous green turning brown, glabrous, sometimes pustulate, single by abortion, containing 50 to 150 seeds; *seeds* flattened, pear-shaped in outline, 6–14 × 3–8 mm, pale beige or yellow to pale brown, with usually somewhat paler margin, slightly papillate, with coma attached at one end except in *F. sinuata* where hairs extend on margin around seed.

One of the defining features of the flower in *Fockea* is the complicated, white, tubular corona with many small lobules projecting inside and around its edges.

This corona starts off as a series of vertical ridges below the lower margins of the anthers (forming the guide-rails), with an outward swelling also occurring below these ridges (Endress & Bruyns, 2000: 18, fig. 9). Gradually three distinct parts appear to this outer corona: a horizontal lobule bridging the gap between the anthers, two diagonal ridges arising from the vertical ridges of the earliest stages, and a further lobule behind and somewhat below each anther. Thus the outer corona consists of 15 lobules. An inner corona of five lobules appears slightly after the first parts of the outer series have begun to swell, and each of these lobes lies behind the anther and a little above the outer series. In more advanced stages these structures become obscured, and the various lobules of the outer corona fuse into a tube. The longest spreading lobules around the mouth of this tube are the ones in the outer series that arose directly behind the anthers. These longest lobules are flanked on either side by a somewhat channel-forming lobule, and these are derived from the two diagonal ridges of the outer series. The remaining lobule of the outer series forms a fairly low bridge between these channel-forming lobules to complete the tubular outer corona. The lobes of the inner corona are fused to the outer corona tube nearly to its apex, and the 'dragged' vascular traces of the anthers show that at least some of the vertical expansion of this tube is achieved by growth at the base of the anther.

In the mature flower in *Fockea*, there is considerable basal fusion between the corona tube and the corolla. As can be seen in Figure 4F and G, the join between the corolla and the corona tube is much higher than that between the corolla and the calyx. However, the ontogeny of the corona shows that this fusion is a later development, and the fact that the vascular trace of the corona branches off from that of the adjacent anther also suggests that this fusion is secondary and does not imply that the corona is contributed to by the corolla, though this was suggested as a possibility by Kunze (1996: 29).

Kunze (1996: 553, figs. 3–5; 554, fig. 12) has shown that the anther in *Fockea edulis* and *F. sinuata* contains endothecial tissue that almost completely surrounds the two locules in each anther. He also found that there is some dorsal dehiscence of the anther, as if it still contained four locules rather than two.

Another defining feature of *Fockea* is the cluster of five soft, erect, inflated, translucent white sterile appendages of the anthers which fill the corona tube (Fig. 4F, G). These appendages only develop their inflated form relatively late. In the early stages there is a distinct separation of the fertile and sterile parts of the anther by slight indentations on either side at the base of the sterile part (Endress & Bruyns, 2000: 18, fig. 9), as is commonly found in the mature anther of the Asclepiadeae. Beneath each appendage the short, roughly square anther is pressed inward onto the style head. The lower margins of the anthers are slightly hardened and hyaline toward their base, forming rudimentary guide-rails just below each corpuscle.

The two ovaries in each flower are together about as broad as tall, and they contain many small ovules (Fig. 4F, G). They are only partly superior, because the ovules continue somewhat below the level of fusion of the calyx and the corolla. The comparatively short style head is sessile on the ovaries. It is broadest at the level at which the corpuscle is secreted, after which it narrows into a short, truncate, and slightly bifid apex that does not exceed the fertile parts of the anthers.

The pollinarium in *Fockea* consists of two small, usually flattened, clear to translucent white, elliptical pollinia and a corpuscle of almost equal size (Fig. 6D, I; Fig. 8G, M, S; Fig. 10H). The pollinia are often so flat that together they make up no more than the thickness of the corpuscle. Kunze (1996: 553, figs. 3, 5) has shown that in *F. sinuata* the pollinium is mostly made up of just two layers of pollen grains, while in *F. edulis* it would appear that only a single layer is present. The corpuscle is pale brown (often only brown and shiny around the top), and it is generally broader when viewed from the side than when seen from above. It is very easily broken into two halves. Near the apex of the corpuscle on the side closest to the style head there is a small process to which both the pollinia are attached, and this may be quite easily visible with the light microscope in some plants. In all species a caudicle joining each pollinium to the corpuscle is lacking. Around its base the structures by which the corpuscle is attached to the style head may be visible as slight protrusions. Kunze (1993) showed that the corpuscle has flanks and a Y-shaped floor that disappears toward the base of the corpuscle.

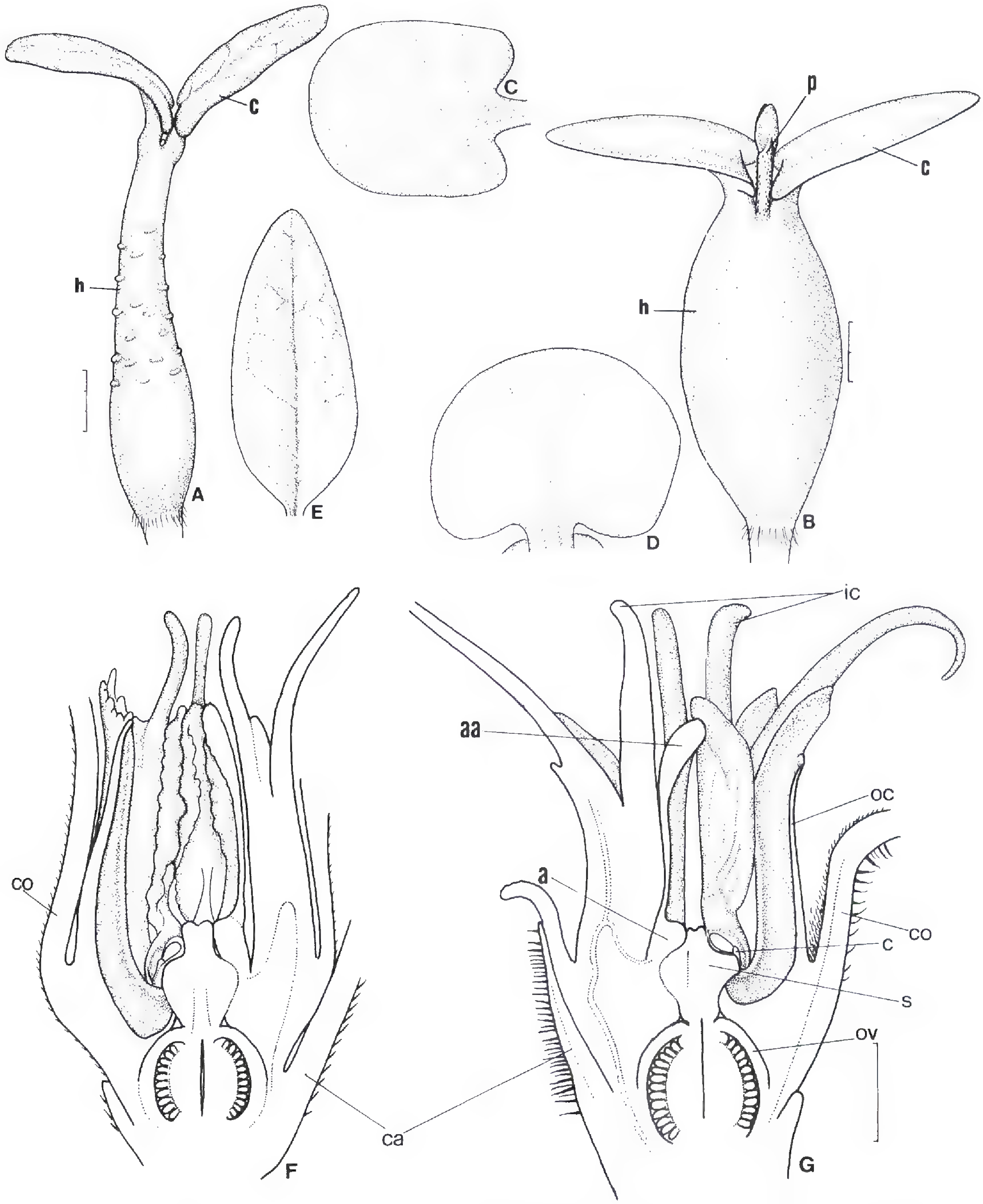

Figure 4. A–E. Seedlings in *Fockea*, about 20 days old. F, G. Half flowers in *Fockea*. —A, B. Side view of plantlet. —C, D. Face view of cotyledon. —E. Face view of one of second pair of leaves. c, cotyledon; h, swollen hypocotyl; p, primary stem; ca, calyx; co, corolla tube; a, anther; aa, sterile anther appendage; oc, outer corona tube; ic, inner corona lobes; c, corpuscle; s, style head; ov, ovary. Drawn from: A, C, E, *F. sinuata*, *Bruyns 3023* (NBG); B, D, *F. edulis*, *Bruyns 4995a* (BOL). F, *F. comaru*, *Bruyns 3329* (BOL); G, *F. edulis*, *Bayer 325* (NBG). Scales: A, C, E = 3 mm (at A); B, D = 2 mm (at B); F, G = 1 mm (at G).

Verhoeven and Venter (2001) found that in *F. angustifolia*, *F. multiflora*, and *F. sinuata* the grains are grouped into tetrads and there is no outer envelope or pollinium wall.

Seedlings (Fig. 4) have been observed in all species of *Fockea* except *F. multiflora*. Each plantlet consists of a swollen, fleshy, green hypocotyl (at least half of which projects from the soil) with two broad, green

cotyledons at the apex. The primary leaves and stem emerge from between the cotyledons after one to three weeks, and the primary leaves are always much narrower than the cotyledons. Swelling of the base of the hypocotyl leads to the formation of the tuber below ground level, while the upper part of the hypocotyl above the soil does not thicken. In species such as *F. comaru* and *F. sinuata*, where the tuber can be up to 20 cm below the surface of the ground, the base of the hypocotyl elongates as well as swells so that gradually the tuber develops well below the surface.

A similarly succulent hypocotyl is common in many of the succulent Asclepiadoideae and is even known in the Periplocoideae in such species as *Ischnolepis graminifolia* (Costantin & Gallaud) Klack., *Sacleuxia salicina* Baill., and *Stomatostemma pendulina* H. Venter & D. V. Field. In the Asclepiadoideae it is found in the Fockeeae in *Fockea*, in the Asclepiadeae in *Sarcostemma* R. Br. and succulent members of *Cynanchum* L., and it is most common in the Ceropegieae (Bruyns, 2000). A succulent hypocotyl is unknown in the Marsdenieae (Forster, 1995).

KEY TO THE SPECIES OF *FOCKEA* (SOUTHERN TO EASTERN AFRICA)

1a. Leaves rarely more than 30 mm long and not more than 20 mm broad; stems arising via narrow neck from distinct basal (mostly subterranean) tuber, stems short and erect or climbing to 1–2 m.
- 2a. Leaves linear, not more than 4 mm broad.
  - 3a. Margins of leaves revolute, leaves with dense adpressed pubescence, outer corona without spreading flap behind each longest terete lobule.
    - 4a. Margins of leaves strongly undulate; corpuscle relatively massive and nearly half as broad as pollinia . . . . 6. *F. sinuata*
    - 4b. Margins of leaves not undulate; corpuscle very slender and much less than half as broad as pollinia . . . . 3. *F. comaru*
  - 3b. Margins of leaves not revolute, leaves with sparse pubescence, outer corona usually with spreading flap behind each longest terete lobule . . . . 1. *F. angustifolia*
- 2b. Leaves elliptic to nearly circular, 6–22 mm broad.
  - 5a. Outer corona without spreading flap behind each longest terete lobule; upper surface of tuber projecting from ground.
    - 6a. Leaves ± glabrous or very sparsely pubescent, margins only slightly undulate. . . . . 4. *F. edulis*
    - 6b. Leaves finely and densely pubescent, margins strongly undulate . . . . 2. *F. capensis*
  - 5b. Outer corona with spreading flap behind each longest terete lobule; tuber well below surface of ground . . . . 1. *F. angustifolia*

1b. Leaves usually more than 30 mm long and 25 mm broad; stems usually massive and often climbing on trees to 10 m or more, plant without distinct basal tuber . . . . 5. *F. multiflora*

1. Fockea angustifolia K. Schum., Bot. Jahrb. Syst. 17: 146. 1893. TYPE: South Africa, Cape, Griqualand West, 48 km W of Kimberley, *G. J. Lewis 67535* (neotype, designated here, PRE!; duplicate, SAM!). Figure 6A–D.

Fockea sessiliflora Schltr., Bot. Jahrb. Syst. 20, Beibl. 51: 44. 1895. TYPE: South Africa. Transvaal, Klippdam, 4500′, 14 Feb. 1894, *F. R. R. Schlechter 4493* (lectotype, designated here, drawing at W, not seen).

Fockea lugardii N. E. Br., Fl. Trop. Afr. 4 (1): 429. 1903. TYPE: Botswana. Ngamiland, Kwebe Hills, *E. J. Lugard 299* (holotype, K!).

Fockea dammarana Schltr., Bot. Jahrb. Syst. 38: 56. 1905. TYPE: Namibia. Damaraland, 1879, *T. J. G. Een* (holotype, BM!).

Fockea tugelensis N. E. Br., Fl. Cap. 4 (1): 778. 1908. TYPE: South Africa. Natal, Tugela, *W. T. Gerrard 1310* (holotype, K!; isotype, BOL!).

Fockea mildbraedii Schltr. in Mildbr., Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot. 2: 545—546. 1913. TYPE: Tanzania. Lembeni, 4 Sep. 1910, *H. J. P. Winkler 3803* (holotype, K!).

Fockea monroi S. Moore, J. Bot. 52: 149. 1914. Type: Zimbabwe. Melsetter distr., Victoria, *Monro 828* (lectotype, designated here, BOL!; duplicate, SRGH).

Cynanchum omissum Bullock, Kew Bull. 10: 623. 1956. TYPE: Kenya. Kwale distr., betw. Samburu & Mackinnon road, 350 m, Aug. 1953, *R. B. Drummond & Hemsley 4045* (holotype, K!).

Small geophytic herb to climber with underground napiform tuber (sometimes somewhat irregularly shaped by pressure of surrounding rocks) up to 50 cm long and 20 cm thick with central growth point on smooth upper surface from which slender perennial and aerial stems arise, stems erect to twining to 1(–2) m, often whitish gray, softer upper parts deciduous, young growth finely tomentose. *Leaves* with petiole 1–3 mm long, grayish to brownish green (often with distinct brownish to purplish hue when young), linear to narrowly elliptic (to circular), 13–65(–105) × (0.5–)1.5–8(–22) mm, obtuse to acute, glabrous to sparsely and finely pubescent (more sparsely below), midrib translucent white, margins slightly to not at all revolute, weakly undulate to straight. *Inflorescence* 1- to 6-flowered, flowers opening in succession, covered with fine adpressed hairs; *peduncle* absent; *pedicels* 1 × 1 mm. *Sepals* 1.5–2 × 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 10–40(–65) mm diam.; outside grayish green, pubescent; inside green to brown, sparsely and finely pubescent; *tube* 1.5–2 mm deep, ca. 2.5 mm broad at mouth, cupular; *lobes* 4–18(–28) × 1–2 mm, linear, obtuse, spreading and often

spiralling to left, often twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming cylindrical tube 4–6 mm long, divided at mouth of tube into 5 longer slender terete and often spreading lobules up to 5 mm long each flanked by 2 flattened spreading lobules, these groups of 3 lobes alternating with 5 linear and usually spreading lobules, longest outer lobes each usually with another flattened spreading lanceolate lobule behind it; *inner corona* of 5 terete linear lobes ca. 3 mm long adpressed to backs of anthers then erect above them. *Follicles* 70–200 × 8–12 mm, gray-green often banded with purple, smooth; *seeds* 8–10 × 4–6 mm, yellow-brown.

Phenology. Flowering October to May.

Distribution. Angola, Botswana, Kenya, Namibia, South Africa, Swaziland, Tanzania, Zambia, and Zimbabwe; 200–1700 m (Fig. 5).

Ecology. Fockea angustifolia occurs in areas receiving rainfall in summer. It is mainly found in stony places, usually on slopes but occasionally in flat areas. In parts of the Kalahari it occurs on stony calcareous flats, while in Tanzania it grows in loamy flat areas.

Discussion. The type (South Africa, Griqualand West, Groot Boetsap, 1200 m, *H. W. R. Marloth 1008*) of Schumann (1893) is missing, and a neotype has been designated here. No material seen by Schumann has been found. Consequently *Lewis 67535* was selected as a neotype, because it is from the same general area as Marloth's missing specimen and is represented in two herbaria. Moore (1914) cited two specimens of Monro in the protologue of *F. monroi*. One of these has been located and is selected as the lectotype. In the case of *F. sessiliflora*, no specimens of *Schlechter 4493* have been located, but a sketch of the flower exists at W and this is selected as lectotype.

K. Schumann (1893, 1895) and Brown (1907–1909) mentioned the name *Brachystelma circinatum* Marloth *non B. circinatum* E. Mey. This appeared in a list of Marloth's collections where, under the Asclepiadaceae, the entry "*Brachystelma circinatum* E. Meyer....bisher von den Witbergen im Kapland bekannt" appeared and the specimen *Marloth 1008* was cited (Engler, 1889: 244). No description or diagnosis was provided nor was any intent of publishing a new name expressed, so the epithet *Brachystelma circinatum* Marloth does not exist (Greuter et al., 2000: ICBN Art. 32.1, Art. 34.1 (a)).

Court (1982) treated *Fockea angustifolia* and *F. comaru* as one species, and they were treated as closely related also in Meve (2002).

Our own investigations revealed that *Fockea angustifolia* and *F. comaru* occur together over a wide area in Namibia and South Africa; the full extent of occurrence is probably still not accurately reflected by the recorded collections. In several cases both *F. angustifolia* and *F. comaru* have been noted on the same farm and have even been seen near each other on the same hillside. So far they have been recorded together in Namibia in the Tiras Mountains and the Great and Little Karas Mountains, while in South Africa they are known to grow together in the hilly southwestern part of Griqualand West. This wide sympatry leads one to suspect that they may not be closely related at all.

Analyses of the molecular data proved our suspicions to be correct. They show that *Fockea angustifolia* and *F. comaru* are two distinct species that are not particularly closely related to one another and that *F. angustifolia* is sister to all the southern species of *Fockea*.

In the areas where they occur together, *Fockea angustifolia* and *F. comaru* look superficially similar. Both are narrow-leaved with slender, often twining stems and a relatively small tuber (at least in comparison to that of *F. edulis*). A number of features can be used to separate them, and they can be distinguished mostly even without flowers. In *F. angustifolia* the main stem generally divides above the surface of the soil. In *F. comaru* the main stem divides mostly well below the surface, so that the stems of a single plant often spread extensively underground and may emerge from the soil some distance away from the central stem. The young leaves of *F. angustifolia* have a noticeably purplish to brownish hue and older leaves are grayish green, while the foliage of *F. comaru* is generally distinctly bluish green. In pressed specimens one finds that the younger stems and leaves of *F. angustifolia* are often very pale to nearly white, while they are dark brown in *F. comaru*. The whole plant in *F. comaru* is covered with fine and often adpressed hairs, while in *F. angustifolia* the hairs are extremely sparse, if present at all. A further feature of the leaves is that their margins are revolute in *F. comaru*, while in *F. angustifolia* they are mostly not revolute (this feature is often distorted by pressing, so that it is not always helpful in herbarium material). Finally, if flowers are present, the two can often be separated on the extra flap in the corona behind each large outer lobe that is usually present in *F. angustifolia* and absent in *F. comaru*.

Specimens examined. ANGOLA. Huila, Sá da Bandeira, *Santos 764* (LISC); E of Oncocua, *Bruyns 10355* (MO); 5 km W of Oncocua, *Bruyns 10363* (E); Iona, *Bruyns 10384* (WIND); near Chapeu Armado, *Bruyns 10406* (K); N of Cahama, *Bruyns 10435* (M).

BOTSWANA. Dobe, *Lee D64/61* (SRGH); 45 km W of Nokaneng, *Bruyns 6479* (BOL); 128 km WNW of Francistown, *Drummond 5283* (SRGH); 81 km W of Kuke gate,

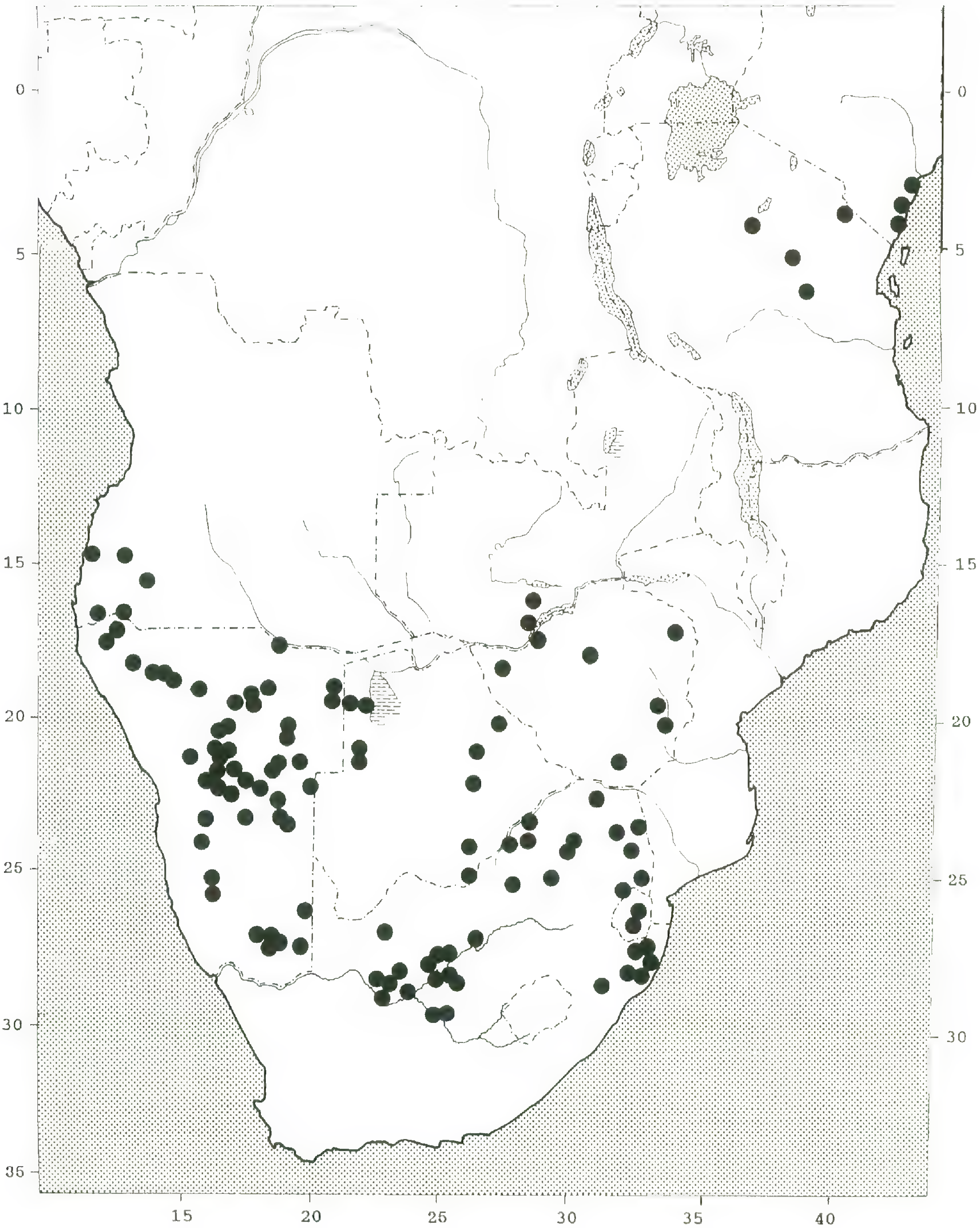

Figure 5. Map of central and southern Africa, showing distribution of *Fockea angustifolia*.

Smith 3167 (K, PRE); 9 km NE of Ghanzi, *Bruyns 6455* (BOL); D'Kar, *Bruyns 6460* (BOL); 8 km W of Lethlekane, *Wild & Drummond 7211* (M, PRE); Makunda, *Gibson 111* (WIND); N of Lephephe, *Snyman & Noailles 222* (PRE); Content farm, *Kelaole 469* (SRGH); Thorn Park, Lobatse, *Bayer 1131* (NBG).

KENYA. 2.5 km E of Dakabuko, *Luke & Robertson 2517* (K); betw. Samburu and Mackinnon Road, *Drummond & Hemsley 4015* (K); Shimba Hills, *Luke et al. 6188* (K).

NAMIBIA. Otjitande, *Rycroft 2460* (NBG); 3 km W of Etengua, *Bruyns 5577* (WIND); SW of Nzinzi, *de Winter 3985* (PRE, WIND); Okorosave, *Owen-Smith 103* (WIND); Kaoko Otavi, *Bruyns 5572* (WIND), *Barnard* (SAM); Orumana, *Grobbelaar 83* (M, WIND); 147 km N of Kamanjab, *Bruyns 4076* (BOL); Etosha Park, Okaumburu, Katspruit, *le Roux 1099* (PRE); Omuramba Onaiso, *Horn* (WIND); 1 miles SW of Okaukeujo, *Le Roux 1258* (WIND); 22 km E of Okakuejo, *Smook 7575* (PRE); Nosib, *Bruyns 2339* (WIND); Kumkauas,

Figure 6. A–D. *Fockea angustifolia*. E–I. *Fockea capensis*. —A, E. Part of flowering branch. —F. Side view of flower. —G. Side view of gynostegium. —B. Side view of dissected gynostegium. —C, H. Side view of anthers. —D, I. Pollinarium. Drawn from: A–D, *Bayer 1431* (NBG); E–I, *Bruyns 2555* (NBG). Scales: A = 3 mm; B = 1 mm (at A); C = 0.5 mm (at A); D = 0.25 mm (at A); E = 5 mm; F = 2 mm (at E); G = 1 mm; H = 0.5 mm (at G); I = 0.25 mm (at G).

Giess & Smook 10639 (M, PRE, WIND); Auros, *Giess 12576* (M, WIND); Gobis Water, *Bruyns 5490* (WIND); 10 km toward Tsumkwe, *Bruyns 4116* (BOL); Grootfontein, *Schoenfelder S 128* (PRE); Sikereti, *Maguire 2267* (BOL, NBG, PRE); near Klein Dobe Camp, *Maggs et al. 1079* (WIND); road to Nyae-Nyae Pan, *Giess et al. 11133* (PRE, S, WIND); road to Makuri, *Hines 910* (PRE, WIND); Gautscha Pan, *Maguire 2193* (BOL, NBG, PRE), *Story 6216* (PRE, WIND);

Ozondjache, *Volk 540* (M); Otjenga, *Volk 1370* (M); Okosongomingo, *Volk 844* (M); Okakarara, *Bartsch 202* (WIND); 24 km NE of Epata, *Giess 9738* (M, WIND); 38 km NE of Epata, *Giess 9751* (WIND); Omaruru, *Bruyns 3611* (WIND); Omatako-Sicht, *Woortman 78* (WIND); Thorntrees, *Immelman 492* (PRE); Omusema, *Kers 2724* (S); Okahandja, *Bradfield 349a* (PRE); Quickborn, *Bradfield 349b* (PRE); Schoongelegen, *Seydel 2594* (M, WIND); Sturmveld, *Tölken 61* (WIND); Wilhelmsruhe, *Bruyns 2273* (WIND), *5474* (K); 64 km N of Gobabis, *Basson 238* (PRE); Epukiro, *Giess 9760* (M, PRE, WIND); Okomitundu, *Seydel 1419* (M, PRE); Ongos, *Kers 2479* (S); Neudam, *Giess 3921* (M, WIND); Ludwig, *Kers 2535* (S); Orumbo-noord, *Giess 8403* (M, PRE, WIND); Gammams, *Wanntorp 91* (PRE); Windhoek, *Dinter 275* (Z); *Hanekom 334* (WIND); *Müller 1420* (PRE, WIND), *Seydel 1704* (WIND); *Pehlemann 1243* (WIND); Voigtland, *Leippert 4355* (M, WIND); Finkenstein, *Wanntorp 185* (S); Nabitsaus, *van Vuuren 585* (M, PRE, WIND); Brack, *Volk 11198* (M); Okasewa, *Dinter 7450* (SAM); Grünental, *Merxmüller 1234* (M); 10 km W of Witvlei, *Burgoyne et al. 5221* (WIND); Witvlei, *Mason & Boshoff 2579* (PRE); Kirschberg, *Bruyns 5470* (WIND); Dawis, *Merxmüller & Giess 1200* (M, PRE, WIND); Oanob Dam Nature Res., *Sievers 168* (WIND); Klein Nauas, *Fleck 898* (Z); 64 km N of Kalkrand, *Acocks 18149* (PRE); Eersbegin, *Bruyns 5463* (WIND); Sandverhaar, *Bruyns 5462* (WIND); Naukluft, *Bruyns 4148* (BOL); Kapokvlakte, Naukluft, *Günsler 9491* (WIND); Duwisib, *Volk 12660* (M); Rooiberg Suid, *Bruyns 5672* (WIND); Barbi, *Bruyns 5709* (WIND); Lovedale, *Bruyns 5727* (WIND); Gaibis, *Bruyns 5445* (WIND); Steinfeld, *Bruyns 8143* (WIND); Dassiefontein, *Mannheimer 653* (WIND); Noachebeb, *Bruyns 5753* (WIND); Garies, *Bruyns 5801* (PRE); *Bruyns 3511* (BOL); Genadendal, *Bruyns 5781* (BOL); *Strohbach et al. 3349* (WIND); 30 km S of Narubis, *De Winter 3314* (PRE).

SOUTH AFRICA. Langkloof, *Leistner 2099* (KMG, PRE); Knockbarragh, Barkly West, *Brueckner 248* (KMG, PRE); Andaluzia, *Herre* (NBG), *Mueller-Stoll* (M); Padkloof, *Acocks 2207* (PRE); Oumeidkloof, Hay, *Cooke 6421* (BOL, KMG); Pauwfontein, *Cooke 6420* (KMG); Hay, *Acocks 2014* (PRE); Rudesheim, *Bruyns 4493* (BOL); Postmasburg, *Esterhuysen 5399* (K); Koopmansfontein, *Acocks 18792* (PRE); Newlands, *Wilman 3165* (KMG); River View, *Acocks 1503* (KMG, PRE); Best Pan, *Tapscott 119* (KMG); Riverton, *Tapscott* (BOL); 48 km W of Kimberley, *Lewis 67535* (PRE, SAM); 51 km W of Kimberley, *Hall 652* (NBG), *Hall 654* (NBG); Waverley, *Bruyns 9425* (NBG); Asbestos Mtns., *Bryant 1096* (PRE); Maselsfontein, *McDonald 77/85* (PRE); Rode Pan, near Orania, *Werger 1324* (PRE); Olifantsrug, *Power 6682* (BOL, K); Driekop, Lückhoff, *van Zyl 1046* (PRE); Magut, *Gerstner 3157* (NH, PRE); 11 km toward Jozini, *Bruyns 4459* (BOL); Nibela store, *Ward & Guy 80* (K, M, PRE); Bangonoma, *Gerstner* (NH); near Muden, *Bruyns 4437* (BOL); Bekamuzi, *Gerstner 3894* (NH, PRE); Umfolozi Game Reserve, *Mthonti 16* (PRE); Mfule Valley, *Venter 5107* (PRE); Hluhluwe Game Reserve, *Ward 2061* (PRE); Masikwaspoort, *van der Merwe 1691* (PRE); Alfred, *Codd 6606* (PRE); Gravelotte, *Bruyns 1920* (NBG); Manyeleti Game Reserve, *Bredenkamp 1784* (PRE); 3 km S of Rooibokkraal, *Leistner 3190* (K, M, PRE); Schwerin, *Leistner 3192* (K, M, Z); 9.5 km SW of Bulge R. *Louw 3545* (PUC); Sterkrivierdam Nature Reserve, *Jacobsen 2809* (PRE); Potgietersrus, *Bolus 11014* (BOL, Z); 58 km N of Marble Hall, *Vorster & Jackson 2160* (PRE); 16 km from Immerpan to Middelburg, *Meeuse 9600* (PRE, S); Kruger Park, *Gertenbach 5446* (PRE); 6.5 km WNW of Rustenburg, *Acocks 19169* (PRE); Hammanskraal, *Mogg 14864* (M, PRE); N of Gomandwane, *van der Schijf & Marais 3644* (PRE); Barberton, *Rogers 20304* (S); Maquassie, *Morris & Engelbrecht 6924/3* (PRE).

SWAZILAND. Sicusha, *Bayliss 564* (K, PRE), *2076* (NBG, Z); St. Phillips, Hlatikulu, *Dlamini* (M, PRE).

TANZANIA. Lembeni, *Winkler 3803* (K); 20 km W of Same, *Bruyns 8672* (K); Ibaya Hill, Mkomazi Game Res., *Vollesen 96/22* (K); Lake Kitangiri, *Richards 13501* (K); 31 km S of Kondoa, *Bruyns 8723* (MO); Chenene Public Land, Dodoma distr., *Rufo & Magogo 719* (K); Kiboriani Hills, *Bruyns 9635* (MO).

ZAMBIA. Gwembe, near Ntoboute village, *Scudder* (SRGH); Sinazongwe, *Bruyns 9587* (MO).

ZIMBABWE. Mwenda, *Jarman* (SRGH); Redlands, *Leach & Gosden 15014* (SRGH); 8 km W of Salt Springs, Sinamatila, *Rushworth 2550* (SRGH); 68 km W of Kadoma, *Bruyns 7454* (BOL); Devure R. bridge, *Chase 7979* (K); Umkondo Mine, *Dale 268* (SRGH); Bubye R., *Drummond 5814* (K, PRE, SRGH).

2. **Fockea capensis** Endl., in Endl. & Fenzl, Nov. Stirp. Dec. 3: 17. 1839. *Fockea crispa* K. Schum. in Engl. & Prantl, Pflanzenfam. 4 (1): 296. 1895. *Fockea edulis* var. *capensis* (Endl.) G. D. Rowley, Asklepios 75: 17. 1998. TYPE: South Africa. Cape, *Boos & Scholl sub Schönbrunn Garden 488* (lectotype, designated here, K!; duplicate, W, not seen). Figures 6E–I.

Perennial herb with large underground to partially exposed tuber to 80 × 60 cm with central growth point on upper warty surface from which a cluster of several more slender perennial and aerial stems arise, stems erect to twining to 1 m with some of more slender growth deciduous, young growth shortly pubescent. *Leaves* with minutely puberulous petiole 1–2 mm long, gray-green, elliptic, 15–30 × 6–12 mm, finely and densely pubescent, acute, margins strongly undulate and crisped but not revolute. *Inflorescence* 1- to 5-flowered, flowers opening in rapid succession, puberulous; *peduncle* 1–2 × 2 mm; *pedicels* 2–6 × 1–2 mm. *Sepals* 1.5–2 × 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 15–22 mm diam.; outside grayish green, puberulous; inside green, puberulous; *tube* 2–3 mm deep, ca. 2 mm broad at mouth, cupular; *lobes* 8–12 × 1.5–2 mm, linear, obtuse, spreading and often spiralling to left, usually twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming cylindrical tube 2.5–3 mm long, divided at mouth of tube into 5 longer slender terete and spreading lobules 2–3 mm long each flanked by 2 flattened spreading lobules, these groups of 3 lobes alternating with 5 truncate to emarginate, usually spreading lobules; *inner corona* of 5 terete linear lobes adpressed to backs of anthers then erect above them and slightly spreading toward tips. *Follicles* 50–80 × 10–12 mm, gray-green, often longitudinally wrinkled; *seeds* 8–10 × 4–6 mm, yellow-brown.

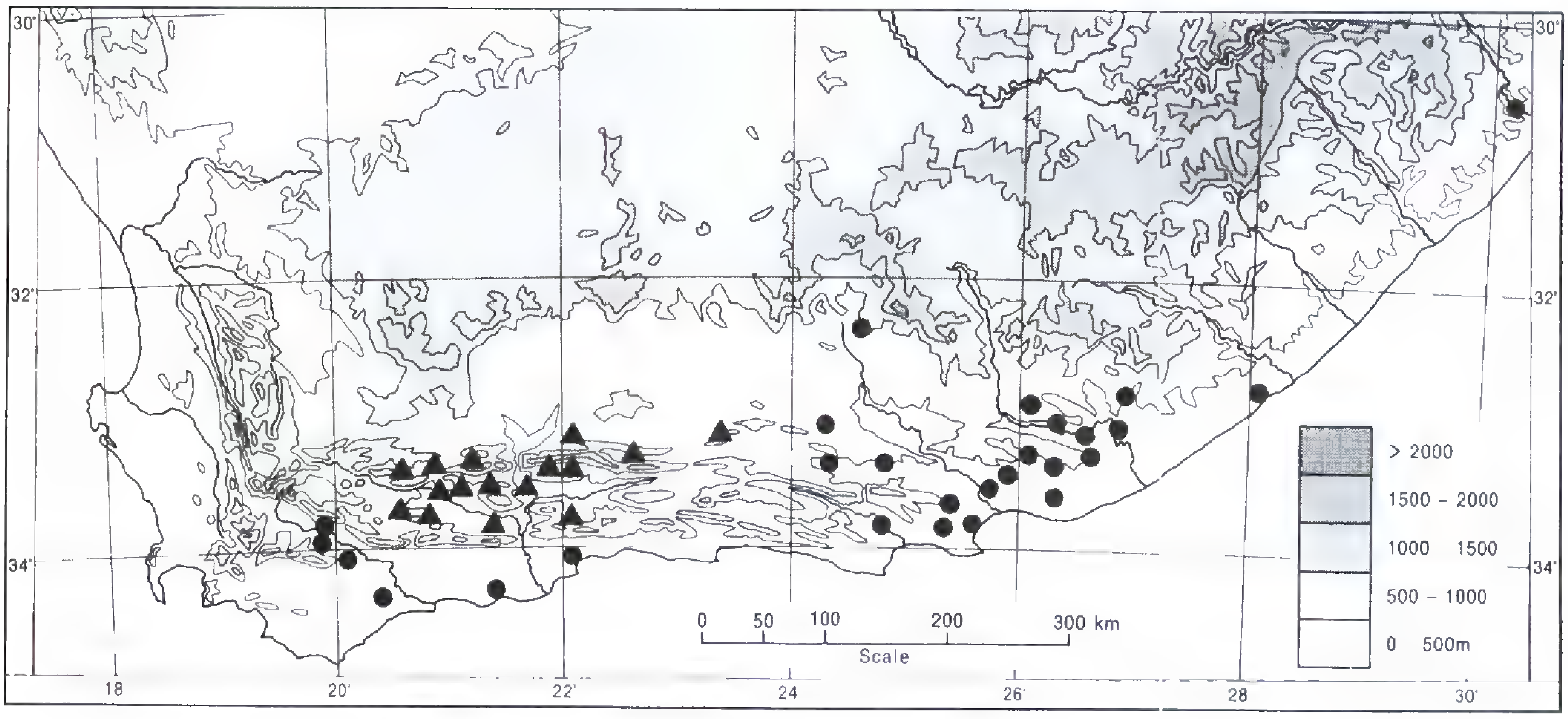

Figure 7. Map of southern Africa, showing distribution of *Fockea capensis* (triangles) and *F. edulis* (circles).

Phenology. Flowering October to May.

Distribution. South Africa; 300–1200 m (Fig. 7).

Fockea capensis is found only in the southern portion of South Africa where it grows on the Little Karoo and in the dry mountains forming its northern border. It has been recorded from a little east of Prince Albert westward on the Little Karoo to the Warmwaterberg (Fig. 7).

Ecology. Specimens of *Fockea capensis* are always found among other succulents on rocky slopes (mostly on sandstones and quartzites but occasionally on shales as well), where the tubers are tightly wedged among the rocks and are often much misshapen by pressure from their surroundings.

Discussion. Endlicher based his description of *Fockea capensis* on the specimen in cultivation at Schönbrunn Gardens but did not cite any preserved material. As only one plant appears to have been grown there, this is assumed to be the same as the specimen *Boos & Scholl sub Schönbrunn Garden 488*, which, consequently, is selected as the lectotype of *F. capensis*.

The name *Fockea crispa* is usually cited with "(Jacq.) K. Schum." as the authors, with *Cynanchum crispum* Jacq. (1800–1809: 31, t. 34) as the basionym (e.g., Court, 1982; Meve, 2002). However, *C. crispum* Jacq. is illegitimate, being a later homonym of *C. crispum* Thunb. (of 1794, which is a synonym of *Brachystelma thunbergii* N. E. Br.). Thus, it cannot be the basionym for any later combination. The first valid publication of the epithet *crispa* for a species of *Fockea* was that of K. Schumann in 1895.

Brachystelma crispum E. Mey. (Meyer, 1838: 196: a later homonym of *B. crispum* Graham, 1830) is sometimes cited as a synonym of *Fockea capensis* (Meve, 2002). However, Meyer (1838: 196) mentioned "*tuber depressum ut in Br. tuberoso... folia 3–4 lineas longa*," so this name applies to a species of *Brachystelma* rather than a species of *Fockea*. The type of *B. crispum*, collected by J. F. Drège (Camdeboo, near Hamerkuil, Meyer, 1838), has not been located, but *F. capensis* does not occur so far to the east in South Africa.

The plants of *Fockea capensis* are not generally as large as those of *F. edulis*. As in *F. edulis*, the distinctly warty upper surface of the tuber usually projects from the ground. Noteworthy in *F. capensis* (and in *F. edulis*) is the frequent presence of a fairly large root spreading outward superficially from near the top of the tuber, which must be important for absorbing moisture close to the surface of the soil. In *F. capensis* the stems are often grazed off so as to be erect, but they may occasionally twine on surrounding bushes, if any are available. The differences from *F. edulis* are discussed under that species.

Specimens examined. SOUTH AFRICA. Skerpkrans, Vrede, *Bruyns 5314* (BOL); Keurfontein, *Bruyns 2809* (BOL); Klein Speeufontein, *Bruyns 4566* (BOL); Spreeufontein, *Bayer 4675* (NBG); 43 km NW of Ladismith, *Bruyns 2555* (NBG); Buffelsrivier Poort, *Bruyns 2554* (NBG); Patatsfontein, *Bruyns 7518* (BOL); Plathuis, *Bruyns 7340* (NBG); nr Warmwaterbron, *Bayer 4676* (NBG); 39 km SE of Laingsburg, *Bruyns 2874* (BOL); Amalienstein, *sub STE 14888* (NBG); Seweweekspoort, *Bruyns 8423* (NBG); Coetzeespoort, *Bruyns 8217* (K); N of Riversdale t'off, *Bruyns 2924* (BOL); 11 km W of Ladismith, *Hall 2592* (NBG); 5 km S of Ladismith, *Bayer & Bruyns 3648* (NBG); Naauwkloof Nat. Reserve, *Hilton-Taylor 900* (NBG); 8 km S of Vanwyksdorp, *Bayer & Bruyns 4674* (NBG); NE of Vanwyksdorp, *Bayer 317* (NBG); Tierberg, near Prince Albert, *Marloth 4465* (PRE, NBG); Boomplaas, *Hugo 21* (NBG), *Moffett 455* (NBG); Droëkloofberge, *Bruyns 8188* (MO); Brakpoort, *Hugo 148* (NBG, PRE); N of Robinson

Pass, *Bayer 458* (NBG); Leeukloof, *Bruyns 7085* (BOL); Boesmanspoortberge, *Bruyns 6315* (BOL).

3. Fockea comaru (E. Mey.) N. E. Br., Fl. Cap. 4 (1): 781. 1908. Basionym: *Brachystelma comaru* E. Mey., Comm. Pl. Afr. Austr.: 195. 1838. TYPE: South Africa. Cape, Nuwerus, N of Beaufort West, *M. B. Bayer 938* (neotype, designated here, NBG!; duplicate, PRE!). Figures 8A–G.

Fockea gracilis R. A. Dyer, Bull. Misc. Inform. 1933: 459. 1934. TYPE: South Africa. Grahamstown, Dikkop Flats, amongst short Karoo bushes, *R. A. Dyer 1251* (holotype, PRE!; isotypes, BOL!, GRA!, K!).

Small geophytic herb with underground napiform tuber (sometimes deformed by rocks) up to 30 × 15 cm with central growth point on smooth upper surface from which slender perennial and aerial stems arise, stems erect to twining to 50 cm (–1 m), softer upper parts deciduous, young growth finely tomentose. *Leaves* with petiole 1 mm long or less, green to bluish green, linear, 25–65 × 1.5–2(–4) mm, obtuse, upper surface darker than lower and finely adpressed pubescent, lower finely pubescent, midrib translucent white, margins strongly revolute, weakly undulate to straight. *Inflorescence* 1- to 6-flowered, flowers opening in succession, covered with fine adpressed hairs; *peduncle* absent; *pedicels* 1–2 × 1 mm. *Sepals* 1.5–2 × 1 mm, lanceolate, outside finely pubescent, inside glabrous; *corolla* 8–27 mm diam.; outside grayish green, finely pubescent; inside gray-green to brown-green, sparsely and very finely pubescent; *tube* 1.5–3 mm deep, ca. 2 mm broad at mouth, cupular; *lobes* 4–12 × 1–2 mm, linear, obtuse, spreading and often spiralling to left, often twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming cylindrical tube 4–6 mm long, divided at mouth of tube into 5 longer slender terete and strongly spreading lobules 2–2.5 mm long each flanked by 2 flattened spreading lobules, these groups of 3 lobes alternating with 5 linear to truncate-emarginate usually spreading lobules; *inner corona* of 5 terete linear lobes adpressed to backs of anthers then rising erect above them. *Follicles* 50–100 × 10–12 mm, gray-green, smooth; *seeds* 8–10 × 4–6 mm, yellow-brown.

Phenology. Flowering October to May.

Distribution. Namibia, South Africa; 100–2000 m (Fig. 11).

Ecology. *Fockea comaru* is always found in stony places on hillsides and mountains, with the tubers often tightly wedged between rocks at a depth of up to 20 cm or more. It is the only species of *Fockea* that is common in the winter rainfall region of the western side of South Africa, where it always occurs with plenty of other succulents. Nevertheless, it is also found well beyond this. Many of the known localities outside the winter rainfall region are in elevated areas (such as the Tiras Mountains and the Great and Little Karas Mountains of Namibia) that receive small amounts of winter rainfall, but those in Griqualand West (for example) do not receive any significant winter rainfall.

Discussion. The specimen cited by Meyer (1838: 195, namely South Africa, Richmond distr., Uitvlugt, near Steelkloof, 4000–5000′, *J. F. Drège*) is missing, and no other suitable specimen of Drège has been located that could serve as a lectotype. Very few collections exist from the central part of South Africa where Drège's specimen came from, and other early collections are neither from this area nor are sufficiently similar to be suitable as neotypes. Consequently a recent collection, *Bayer 938*, is selected as neotype.

Although the stems in *Fockea comaru* may climb in surrounding bushes, they are often short and erect and frequently do not twine at all, forming instead small rosettes on the ground. The stems have a rhizomatous habit and often spread underground for some distance from the tuber before emerging from the soil. These subterranean stems appear to be perennial. In such situations, stems from the same plant may appear over a considerable distance, giving the appearance of several specimens growing near each other, though, on excavation, they prove to originate from the same tuber.

As shown in Fig. 8A–G, the flowers are exceptionally variable in diameter and the lobes may be quite short and not twisted at all.

Apart from the highly succulent stapeliads, asclepiads are not generally common in the winter rainfall parts of southern Africa. In this respect *Fockea comaru* (along with a few species of *Microloma*) is unusual, and it is of very wide and quite frequent occurrence in these areas. The very narrow, linear leaves and the milky sap make the plants of *F. comaru* unmistakable among the asclepiads in most areas where they occur. It is often well known where it occurs, with the tubers being dug out and consumed, and the plants are known as *kambroo* or *bergkambroo*.

The molecular data (e.g., Fig. 3) show that *Fockea comaru* and *F. sinuata* are very closely related and scarcely differ at all in the three gene regions investigated. Morphological differences between the two are discussed under *F. sinuata*.

In our molecular sampling, we included an accession of the former *Fockea gracilis* (*Dold 2381*), and this did not group strongly with the other accession of *F. comaru*. *F. gracilis* was mainly

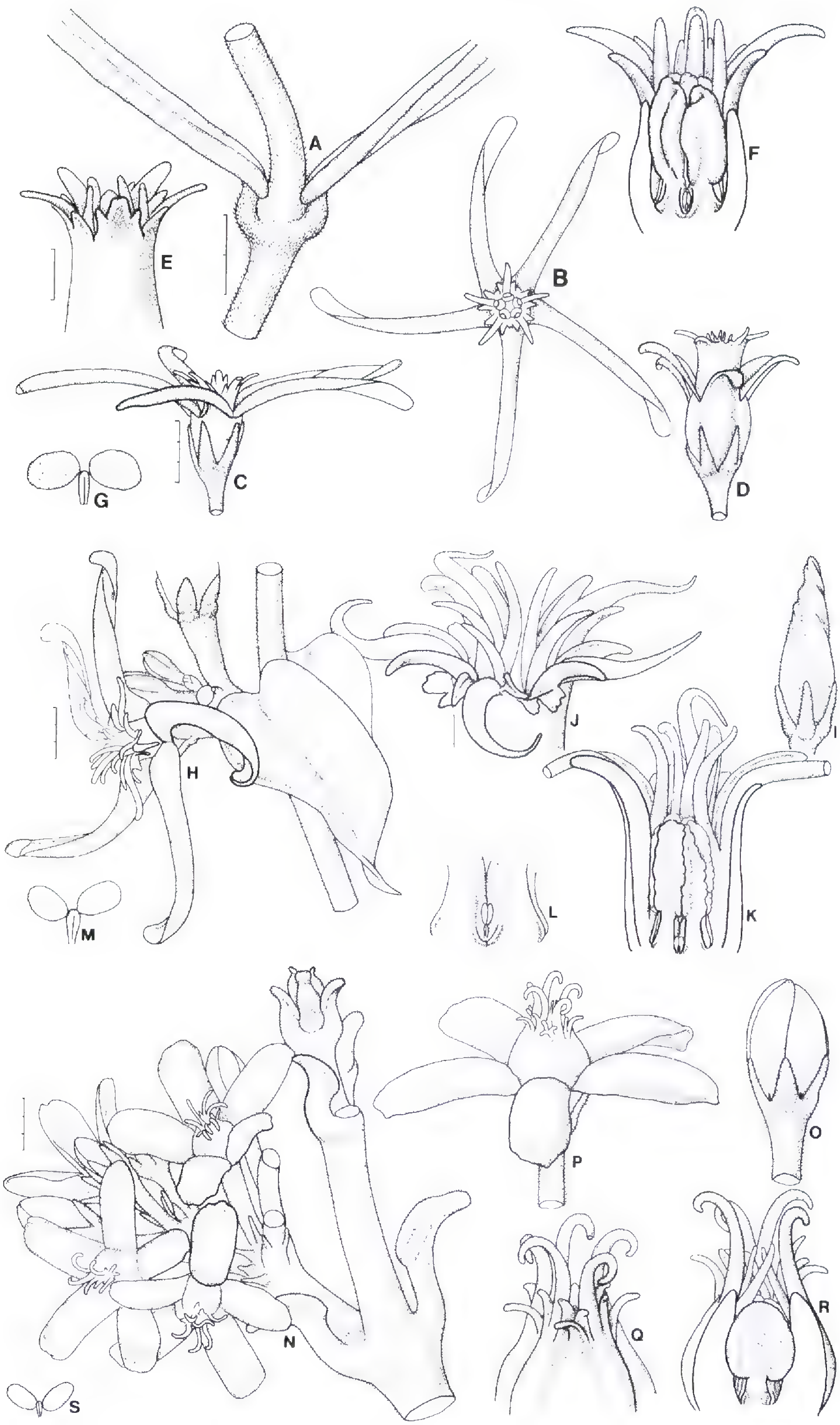

Figure 8. A–G. *Fockea comaru*. H–M. *Fockea edulis*. N–S. *Fockea multiflora*. —A, H, N. Portion of stem. —I, O. Bud. —B. Face view of flower. —C, D, P. Side view of flower. —E, J, Q. Side view of gynostegium. —F, K, R. Side view of dissected gynostegium. —L. Side view of anthers. —G, M, S. Pollinarium. Drawn from: A–C, E, F, *Bruyns 1700a* (NBG); D, E, *Bruyns 3129* (BOL); G, *Bruyns 3107* (NBG); H–M, *Bayer 325* (NBG); N–S, *D. Laing* (K). Scales: A = 2 mm; B–D = 3 mm (at C); E = 1 mm; F = 1 mm (at C); G = 0.25 mm (at C); H, I = 3 mm (at H); J, K = 1 mm (at H); L = 0.5 mm (at H); M = 0.25 mm (at H); N = 3 mm; O, P = 2 mm (at N); Q, R = 1 mm (at N); S = 0.25 mm (at N).

distinguished from *F. comaru* by its much smaller flowers. However, the wide variation in this feature within *F. comaru* makes *F. gracilis* impossible to recognize reliably, so that we are unable to distinguish it from *F. comaru*. Molecular support for its distinctness from *F. comaru* is also negligible (Fig. 3).

Specimens examined. NAMIBIA. Landsberg, *Bruyns 8112* (WIND); Naus, *Bruyns 5698* (WIND); Lovedale, *Bruyns 5724* (WIND); Tschaukaib, *Bruyns 3170* (NBG); Nooitgedacht, *Bruyns 8348a* (WIND); Nasapberg, *Bruyns 7206* (NBG); Sebrafontein, *Bruyns 3924* (BOL); Steinfeld, *Bruyns 8142* (WIND); Lord Hill, *Bruyns 8147* (WIND); Witmond, *Bruyns 5759* (WIND); *Strohbach et al. 3800* (WIND); Garies, *Bruyns 5805* (PRE); *Bruyns 3512* (WIND); Genadendal, *Bruyns 5783* (BOL).

SOUTH AFRICA. Kodaspiek, *Bruyns 8278* (K); Van Der Sterrberge, *Bruyns 7281* (NBG); summit Rosyntjie Mtn., *Bruyns 3291* (NBG); summit Cornellsberg, *Bruyns 3304* (NBG); 6 km S of Eksteenfontein, *Bruyns 8286* (MO); Kliphoogte, *Herre sub STE 12334* (NBG); Rudesheim, *Bruyns 4493* (BOL); Steinkopf, *Marloth 13300* (PRE); Hester Malan Reserve, *Rösch & le Roux 729* (PRE); Gannapoort, *Leistner 2447* (K, KMG, PRE); Waverley, *Bruyns 9424* (MO); Strydenburg, *Hall 640* (NBG); 6 km N of Ou Dam, *Bruyns 6753* (BOL); 4 km W of Paulshoek, *Bruyns 6107* (PRE); N of Kaams, *Bruyns 6348* (BOL); Stofkraal, *Bruyns 4767* (BOL); Witvlakte Oos, *Bruyns 6089* (PRE); Kubiskow, *Bruyns 6085* (PRE); Loeriesfontein, *Marloth 12848* (PRE); Nooiensberg, *Bruyns 6645* (BOL); NW of Komkans, *Bruyns 6255* (BOL); Nuwerus, *Bruyns 6786* (BOL); Kalkgat Noord, *Bruyns 6018* (BOL); 16 km S of Klawer, *Hall sub NBG 817/48* (NBG); Eselskop, *Bruyns 6824* (BOL); Blomberg, *Bruyns 7859* (NBG); Calvinia, *Marloth 7147b* (PRE); Kliprug, *Bruyns 6056* (PRE); Botterkloof, *Bruyns 6038* (PRE), *Hall 700* (NBG); Aarkolk, *Bruyns 5980* (BOL); Grootfontein, *Coetzer 59* (PRE); Boesmansberg, Juriesfontein, *Bruyns 6688* (BOL); Nuwerus, *Bayer 938* (NBG, PRE); Pakhuis, *Hall sub NBG 45/50* (NBG); Clanwilliam Dam, *Bruyns 6034* (PRE); 11 km SE of Redelinghuis, *Bruyns 4734* (BOL); 6 km N of Het Kruis, *Bruyns 6175* (BOL); E of Uitspankraal, *Bruyns 7502* (NBG); Bossiesberg, *Bruyns 7572* (BOL); 2 km N of Uitsig, *Bruyns 6708* (BOL); Aarfontein, *Bruyns 6361* (BOL); Klipfontein, *Bruyns 3107* (NBG); Amandelboom, *Bruyns 6695* (BOL); Doornhoek, *Bruyns 3991* (BOL); Prutkraal, *Bruyns 3141* (BOL), *Snyman* (NBG); Worcester Veld Reserve, *Olivier 255* (PRE); 19 km SE of Worcester, *Bayer 319* (NBG); 4 km W of Robertson, *Schwegmann* (NBG); 2 km SW of Robertson, *Bayer 136* (NBG); Doornrivier, *Stokoe* (PRE); Avondrust, *Bayer 318* (NBG); Whitehill, *Archer 18286* (BOL); Ou Tol, *Bruyns 6304* (BOL); Plathuis, *Bruyns 7341* (NBG); Coetzeespoort, *Bruyns 8216* (NBG); Calitzdorp, *Oddie 559/36* (BOL); Prince Albert, *Marloth 7147a* (PRE); Haggas, *Vlok 2440* (NBG); Vleikuil, *Bruyns 6309* (BOL); Skietkuil, *Bruyns 3129* (BOL); Zuurbergpoort, *Hall 1645* (NBG); near Steytlerville, *Compton 4998* (NBG); Korhaan Vlakte, Addo, *Dold 2381* (GRA, PRE); Dikkop Flats, *Dyer 1251* (BOL, GRA, PRE); 4 km NW of Stormsvlei Pass, *Bayer 329* (NBG).

4. **Fockea edulis** (Thunb.) K. Schum., Bot. Jahrb. Syst. 17: 146. 1893. Basionym: *Pergularia edulis* Thunb., Prodr. Pl. Cap. 1: 38. 1794. *Echites edulis* (Thunb.) Thunb., *In genus Echitis observationes*: 5. 1819. TYPE: South Africa. Cape. Gouritz River, *C. P. Thunberg 6141* (holotype, UPS, not seen). Figure 8H–M.

Brachystelma macrorrhizum E. Mey., Comm. Pl. Afr. Austr.: 197. 1838. TYPE: South Africa, Cape, Graaff-Reinet, *Marloth 7048* (neotype, designated here, PRE).

Fockea glabra Decne. in DC. Prodr. 8: 545. 1844. TYPE: South Africa. Cape, *C. L. P. Zeyher 239* (holotype, P!; isotypes, G, not seen, W, not seen).

Fockea cylindrica R. A. Dyer, Bull. Misc. Inform. 1933: 459. 1934. TYPE: South Africa. Cape, Fish River Valley, near Committees, amongst karroid scrub on dry flats, *R. A. Dyer 1635* (holotype, K!; isotypes, GRA!, PRE!).

Perennial herb with large underground to partially exposed tuber up to 50 cm long and 1 m broad with central growth point on upper usually warty surface from which 1 to several more slender perennial and aerial stems arise, stems erect to twining to 2 m with some of more slender growth deciduous, young growth puberulous. *Leaves* with minutely puberulous petiole 2–8 mm long, green often with paler midrib, elliptic, 15–45 × 6–20 mm, glabrous to sparsely pubescent, acute, margins often undulate but not revolute. *Inflorescence* 1- to 8-flowered, flowers opening in succession, puberulous; *peduncle* 1–3 × 1 mm; *pedicels* 1–3 × 1 mm. *Sepals* 1.5–2.5 × 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 10–22 mm diam.; outside grayish green, sparsely puberulous; inside green, glabrous to puberulous; *tube* 2–5 mm deep, ca. 3 mm broad at mouth, cupular; *lobes* 6–12 × 1.5–2 mm, linear, obtuse, spreading and often spiralling to left, usually twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming cylindrical tube 3–4 mm long, divided at mouth of tube into 5 longer slender terete and ascending to strongly spreading lobules 2–3 mm long each flanked by 2 flattened spreading lobules, these groups of 3 lobes alternating with 5 linear to truncate to emarginate usually spreading lobules; *inner corona* of 5 terete linear lobes adpressed to backs of anthers then erect above them and slightly spreading toward tips. *Follicles* 50–80 × 10–12 mm, gray-green, often longitudinally wrinkled; *seeds* 8–10 × 4–6 mm, yellow-brown.

Phenology. Flowering October to May.

Distribution. South Africa; 10–1200 m (Fig. 7).

Ecology. *Fockea edulis* is found in dry bush in the southern portion of South Africa, from the Worcester-Robertson Karoo and the coastal plain east of Bredasdorp to around East London and also in similar habitats in southern Natal around the Oribi Gorge. Plants occur among rocks and bushes or trees on slopes. It is rather more rarely found in flat areas,

as in the low-lying areas between Steytlerville and Port Elizabeth.

Discussion. In both Schumann (1893: 146) and Schumann (1895: 296), "*Fockea edulis* (Thbg.) K. Sch." is mentioned, and no attempt is made to describe this as a new species. Consequently in Schumann (1893: 146) a valid new combination was made, because he made an indirect reference to a previously published name (Greuter et al., 2000: ICBN Art. 32.4, Art. 32.5) and the basionym for this name is *Pergularia edulis* Thunb. as given in Brown (1907–1909: 780).

For *Brachystelma macrorrhizum*, Meyer (1838: 197) cited an unnumbered collection of Drège (South Africa, Oudeberg mountain), which is missing. The neotype selected here is from the same area as Drège's collection, so that this name is unequivocally a synonym of *Fockea edulis*.

As mentioned above, Harvey (1842) made no new combinations in *Chymocormus* even though he mentioned *Pergularia edulis* as belonging to this new genus. Consequently *C. edulis* (as given in Schumann, 1895; Brown, 1907–1909; and Meve, 2002), is not valid (Greuter et al., 2000: ICBN Art. 33.1) and is not cited here.

In more bushy areas *Fockea edulis* is a vigorous climber to a height of 2 m. In more arid spots, where the vegetation is altogether shorter (such as on the Worcester-Robertson Karoo), *F. edulis* can be a small and inconspicuous climber among bushlets of *Carissa bispinosa* (L.) Desf. ex Brenan and other species. Even smaller, tufted plants that scarcely twine at all are characteristic in areas of low, mostly succulent vegetation between Steytlerville and Port Elizabeth, and one of these was described as *F. cylindrica* [= *F. edulis*].

In *Fockea edulis* the distinctly warty upper surface of the tuber usually projects slightly from the ground. The tuber may be enormous and has been recorded up to 1 m in diameter (*Bayer 326*, NBG).

Fockea edulis and *F. capensis* are similar in many respects. Both have comparatively broad leaves (6–20 mm broad in comparison to 1.5–4 mm broad in *F. comaru*) and large tubers with the upper surface projecting from or level with the surface of the ground. *Fockea capensis* is short and shrubby in habitat, but the stems will twine if provided with the opportunity. In *F. capensis* the leaves have distinctly undulate or crisped margins and are densely covered with adpressed hairs, while in *F. edulis* the leaves have at most slightly undulate margins and are more or less glabrous. This lends them a green color in *F. edulis* and a distinctly gray-green color in *F. capensis*. Florally there are no significant differences between them. This close relationship is reflected in Figure 3.

Specimens examined. SOUTH AFRICA. SW side of Graaff-Reinet, *Burchell 2916* (K); Tandjiesberg, *Bruyns 2976* (BOL); Graaff-Reinet, *Marloth 7048* (PRE); Adelaide road, *J.-Guillarmod 4929* (PRE); Keiskamma, *Bayer 323* (NBG); Gonubie Mouth, *Bayer 326* (NBG); Klaasvoogds, *Bayer 325* (NBG); Rooiberg, Goudmyn, *Bruyns 6793* (BOL); Klipplaat, *Bayer* (NBG); Witkop, *Desmet 2240* (NBG); Kleinspoort, *Bayer* (NBG); Ventershoek, *van Jaarsveld 11410* (NBG); Addo Elephant Park, *Botha 5800* (PRE); near Groendal, *Vlok 554* (PRE); 36 miles from Port Elizabeth to Steytlerville, *Long 1184* (K); Springs Reserve, Uitenhage, *Olivier 2495* (PEU); Uitenhage, *Zeyher 965* (K); near Uitenhage, *Burchell 4450, 4443, 4457* (K); betw. Port Elizabeth and Uitenhage, *Long 1469* (K); Addo, *Acocks 13661* (PRE), *Kreft 96* (BOL); Coega, *Bayer 320* (NBG), *Bursey* (NBG), *Olivier 1577* (PRE); Bluewater Bay, *Olivier 3042* (PRE); Swartkops, *Hallack 3052* (PRE); Humewood, *Dahlstrand 60* (PRE); Redhouse, *Paterson 544* (BOL, Z); Aloes stn., *Long 903* (K); Hounslow, *Galpin 13250* (BOL, PRE), *13251* (P, PRE); near Hyde's Hill, *Nicholas 912* (PRE); betw. Tootabi and Alicedale, *Archibald 5984* (PRE); 10 miles from Grahamstown toward Alexandria, *Dyer 956a* (K); Ecca Pass, *Bayer* (NBG); Pluto's Vale, *Bayer 322* (NBG); Trumpeter's Drift, *Story 2190* (PRE); Adelaide road, *Jacot Guillarmod 4929* (PRE); Nook Boosaak Forest, Alexandria, *Britten 2506* (PRE); N of Stormsvlei Pass, *Bayer* (NBG); De Hoop, *Bruyns 6656* (BOL); Kafferkuils R. mouth, *Muir 149* (PRE); Klein Brakrivier extension 4, *Taylor 8341* (NBG); Gibraltar rock, *Nicholson & Strey 1968* (PRE), *Balkwill 439* (NU).

5. Fockea multiflora K. Schum., Bot. Jahrb. Syst. 17: 145. 1893. TYPE: Tanzania. French mission in Ussambiro, *F. L. Stuhlmann 848* (holotype, B, missing; isotype, K!). Figure 8N–S.

Fockea schinzii N. E. Br., Bull. Misc. Inform. 1895: 259. 1895. TYPE: Angola. *F. Welwitsch 4194* (lectotype, designated here, K!; duplicate, P!).

Large climber to 15 m, with stout trunk (to 30 cm thick) sprawling on ground or twisting around trees for support, rarely shrub-like; stems fleshy and becoming swollen toward base but without distinct basal tuber, young stems tomentose and slightly fleshy, remaining fleshy but becoming covered with gray, shiny bark. *Leaves* with petiole 8–25(–45) mm long, gray-green, oblong to broadly elliptic, (20–)30–150 × (10–)25–100 mm, often apiculate, upper surface tomentose to glabrous, lower tomentose with raised midrib and veins, margins not revolute or undulate. *Inflorescence* (6- to)10- to 30-flowered, flowers opening ± simultaneously or in rapid succession, pubescent; *peduncle* 5–15 × 2–5 mm; *pedicels* 5–13 mm long. *Sepals* 2–3 × ca. 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 10–15 mm diam.; outside grayish green, pubescent; inside yellowish green to brown, glabrous to sparsely pubescent; *tube* 1.5–2 mm deep, ca. 3 mm broad at mouth, shallowly cupular; *lobes* 5–10 × 2 mm, broadly linear, obtuse, spreading, with margins and apex slightly reflexed; *corona* white,

glabrous; *outer corona* forming tube 2–3 mm long, becoming distinctly narrower above anthers, divided at mouth of tube into 5 longer slender terete spreading lobules 2–2.5 mm long each flanked by 2 flattened slightly spreading lobules, these groups of 3 lobes alternating with 5 linear recurved lobules; *inner corona* of 5 flattened linear lobes adpressed to backs of anthers then intertwined above them. *Follicles* 100–220 × 15–30 mm; *seeds* 10 × 7–8 mm.

Phenology. Flowering August to December.

Distribution. Angola, Botswana, Moçambique, Namibia, Tanzania, Zambia, Zimbabwe; 600–1000 m (Fig. 9).

Ecology. Fockea multiflora occurs in rocky areas on low hills or among rocks around the base of hills in open, often deciduous woodland consisting of an *Acacia-Commiphora-Balanites* association or *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léon. Plants are usually common.

Discussion. The specimen at B on which K. Schumann based *Fockea multiflora* was destroyed during World War II. However, some of the same collection is preserved at Kew and this is selected as an isotype. For *F. schinzii*, Brown (1895) cited *Welwitsch 4194* and an unnumbered collection of Schinz, which has not been located. The Welwitsch collection is selected as lectotype.

Fockea multiflora is by far the largest species, and massive specimens are probably the largest known asclepiads. The big fleshy stems sprawl on the ground or twist up the trunks of surrounding trees as massive lianes and appear to strangle them, though there is no evidence that they have any detrimental effect on these trees. Damaged specimens sometimes form a huge mass of entangled stems without any longer climbing stems, but this is exceptional. In all the other species of *Fockea*, the stems arise from a tuber that is much broader than the main stem. In *F. multiflora*, although the young plants have a thickened base, this generally disappears with age, so that in mature specimens there is no basal tuber and the rootstock consists of a network of fleshy roots radiating from the base of the stem. Only the youngest shoots and the leaves are deciduous, while the remainder of the plant is perennial. The leaves are also much larger (to 15 × 10 cm) than those of any other species of *Fockea*. The large size extends into the fruit and the seeds.

Fockea multiflora is unusual in that the inflorescences arise in large numbers around the end of the dry season between August and October (more rarely in December), on young growth produced before the true growing season begins. The sweetly scented flowers appear on the first young shoots of the new growing season among small, under-developed leaves and are sometimes used as a vegetable (*B. L. Burtt 1520* (K); Bruyns & Klak, pers. obs., Gulwe district, Tanzania). Several features of the flower are unique. They are produced in dense, more or less simultaneously opening clusters. The corolla lobes are comparatively short and relatively broad (unlike the other species where they are mostly slender and linear) and are not twisted along their length (Fig. 8N, P). The corona tube is often also noticeably constricted toward the mouth (Fig. 8P, Q). Both the corona tube and the comparatively broad anther appendages are also relatively short (Fig. 8R).

Specimens examined. ANGOLA. Bibala, *Gossweiler 13131* (LISC); Gambos, *Borges 308* (LISC, PRE, SRGH), *Pearson 2134* (BOL); Humbe, *Menezes & Sousa 3423* (LISC, PRE); Mupa, *Menezes 3152* (LISC, PRE, SRGH); Xangongo, *Santos & Barrosa 2825* (LISC, PRE); Ondjiva, *Menezes 1017* (LISC).

BOTSWANA. Ngoma on Chobe R., *Miller 1050* (PRE), *Story 4809* (P, PRE), *Munro sub PRE 6924* (PRE); Okavango, near Nokaneng, *Tinley sub PRE 51262* (PRE).

MOÇAMBIQUE. About 17 km from Mágoè toward Mágoè Velho, *Tôrre & Correia 18156* (LISC); 17 km from Zimbabwe border in Mazoe R. area, *Wild 2584* (SRGH); about 6 km from Changara, *Tôrre & Correia 18709* (LISC).

NAMIBIA. Near Ombepera, *Gibson 219* (WIND); Omupanda, *Rautanen* (Z); Ondangua, *Smuts & Pole Evans 2238* (PRE); Olukonda, *Rautanen 161* (Z); Impalela Island, *Pienaar 201a* (PRE); 6 km NE of Opuwo, *Kolberg et al. 771* (WIND); Kaoko Otavi, *Owen-Smith 128* (WIND); 7 km S of Okaruwizu, *Giess & Wiss 3310* (M, PRE, WIND); Andara Mission Stn., *de Winter & Wiss 4430* (M, PRE, WIND); Popa Falls, *Maggs 632* (WIND); Halali, *Giess 15309* (WIND); Tsumeb, *Nägelsbach 18D* (PRE); Heidelberg, *Walter 563* (WIND); 10 km N of Tsumeb, *v. Jaarsveld 3093* (NBG); 7 km SW Tsumeb, *Hardy 2122* (PRE, WIND); Ombanje, *Schinz 5* (K), *Schinz 146* (Z); Huisib Mtn., *Hilbert 31* (WIND); Strijdfontein, *Dinter 684* (SAM); Grootfontein, *Schoenfelder 5203* (PRE); *Wettstein 280* (M).

TANZANIA. E of Kakesyo, *Greenway 9056* (EA, PRE); S of Kakesyo, *Greenway 9057* (EA, PRE); N end of Lake Eyassi, *Bally 11626* (K); Lake Kitangiri, *Richards 13490* (K); Mkalama, *Burtt 293* (K); 12 miles from Singida to Itigi, *Richards 20001* (K); hills SW of Kondoa, *Burtt 1454* (K); near Dodoma, *Rigby 73* (EA); Chipogolo, *Johannson 1140* (K); Mpwapwa, *Hornby 2111* (EA); Utengule-usangu, *Leedal 2355* (EA); Noubardad, *Newbold 6307* (EA); Lake Eyasi, *Bally 10617* (EA); Badugu, Nasso, Mwanza, *Tanner 1085* (K); E of Lake Eyassi, near Mongala, *Verdcourt 4014A* (K); Magungila, Singida distr., *Burtt 1520* (K); Mtera Dam, *Bruyns 9613* (PRE); S of Mpapwa, *Bruyns 9646* (NBG); S of Gulwe, *Bruyns 9651* (E).

ZAMBIA. Luangwa Valley, *Astle 5149* (SRGH), *Trapnell 1877* (EA); Bombwe Forest Office, *Bombwe 318/32* (EA); Bombwe, *Martin 318* (K); Nkoata Isl., Mkupa, *Bullock 1186* (K); Gwembe Valley, Mazubuka distr., *Bainbridge 139/55* (K); Sinazongwe, *Bruyns 9586* (E); Monza, *Bruyns 9593* (MO).

ZIMBABWE. Chirundu, *Wild 4852* (PRE, SRGH); just S of Zambesi R. on Mazabuka–Harare rd., *Levy sub PRE 36784* (PRE); Mensa Pan, 18 km ESE of Chirundu Bridge, *Drummond 5363* (PRE, SRGH); Copper Queen purchase area, *Bingham 872* (SRGH); 35 km N of Gokwe, *Goldsmith*

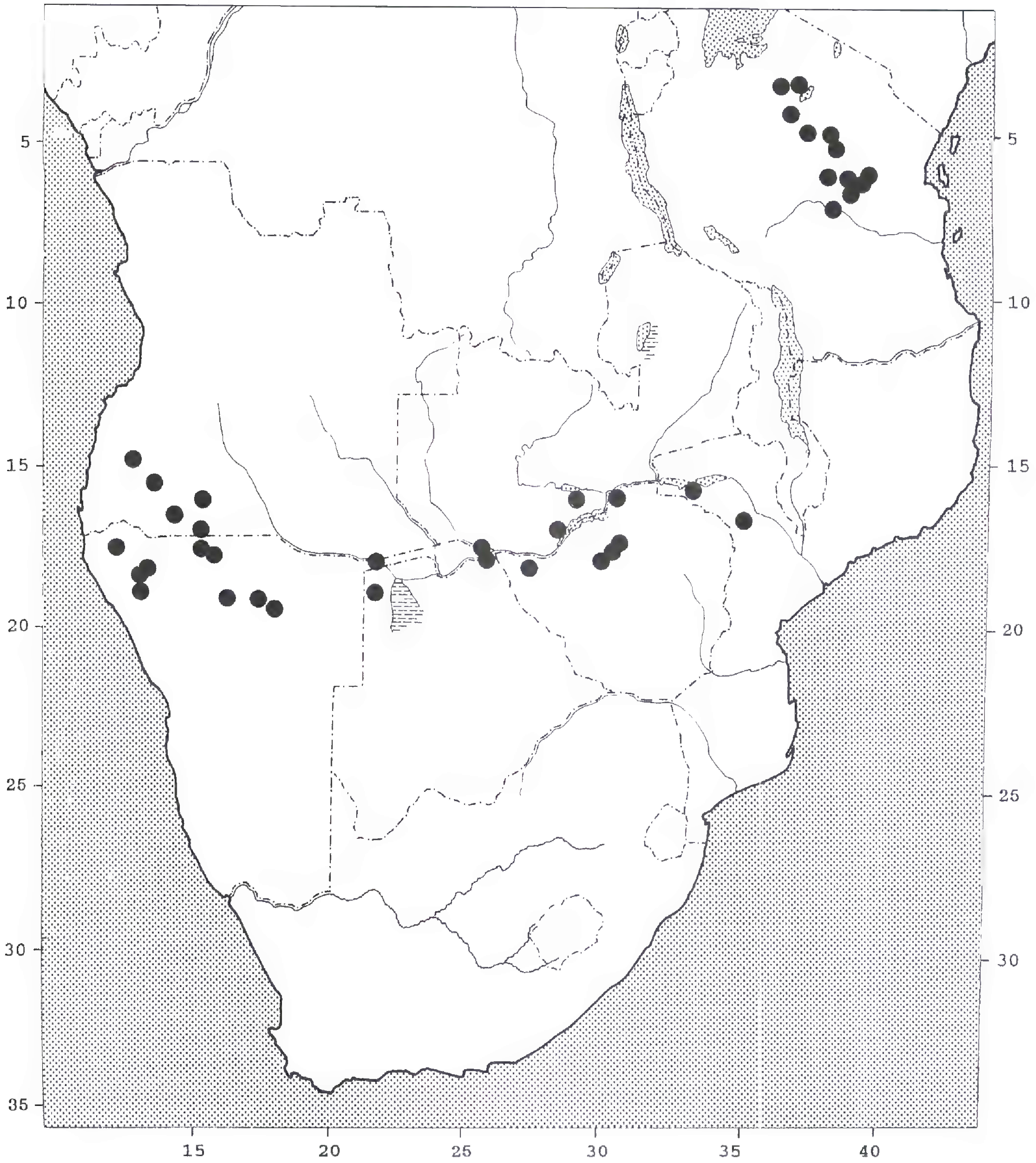

Figure 9. Map of central and southern Africa, showing distribution of *Fockea multiflora*.

21097 (SRGH); Wankie, *Levy 1123* (SRGH); betw. Sesami R. and Gokwe, *West 2998* (SRGH).

6. **Fockea sinuata** (E. Mey.) Druce, Bot. Soc. Exch. Club Brit. Isles: 623. 1917. Basionym: *Brachystelma sinuatum* E. Mey., Comm. Pl. Afr. Austr.: 196. 1838. TYPE: South Africa. Cape, Brakvallei, betw. Kat River & Swart River, 3500′, 15 Jan. 1827, *J. F. Drège 3439B* (lectotype, designated here, P!; duplicate, K!). Figure 10.

Fockea undulata N. E. Br., Bull. Misc. Inform. 1895: 260. 1895. TYPE: South Africa. Cape "Transvaal", Rhenosterkop, *J. Burke* (holotype, K!).

Small geophytic herb with underground napiform tuber to 30 × 10 cm with central growth point on upper surface from which slender perennial and aerial stems arise, stems erect to weakly twining to 45 cm, softer upper parts deciduous, young growth tomentose. *Leaves* sessile, brown- to gray-green, linear, 25–65 × 2–4 mm, obtuse, upper surface darker and adpressed-

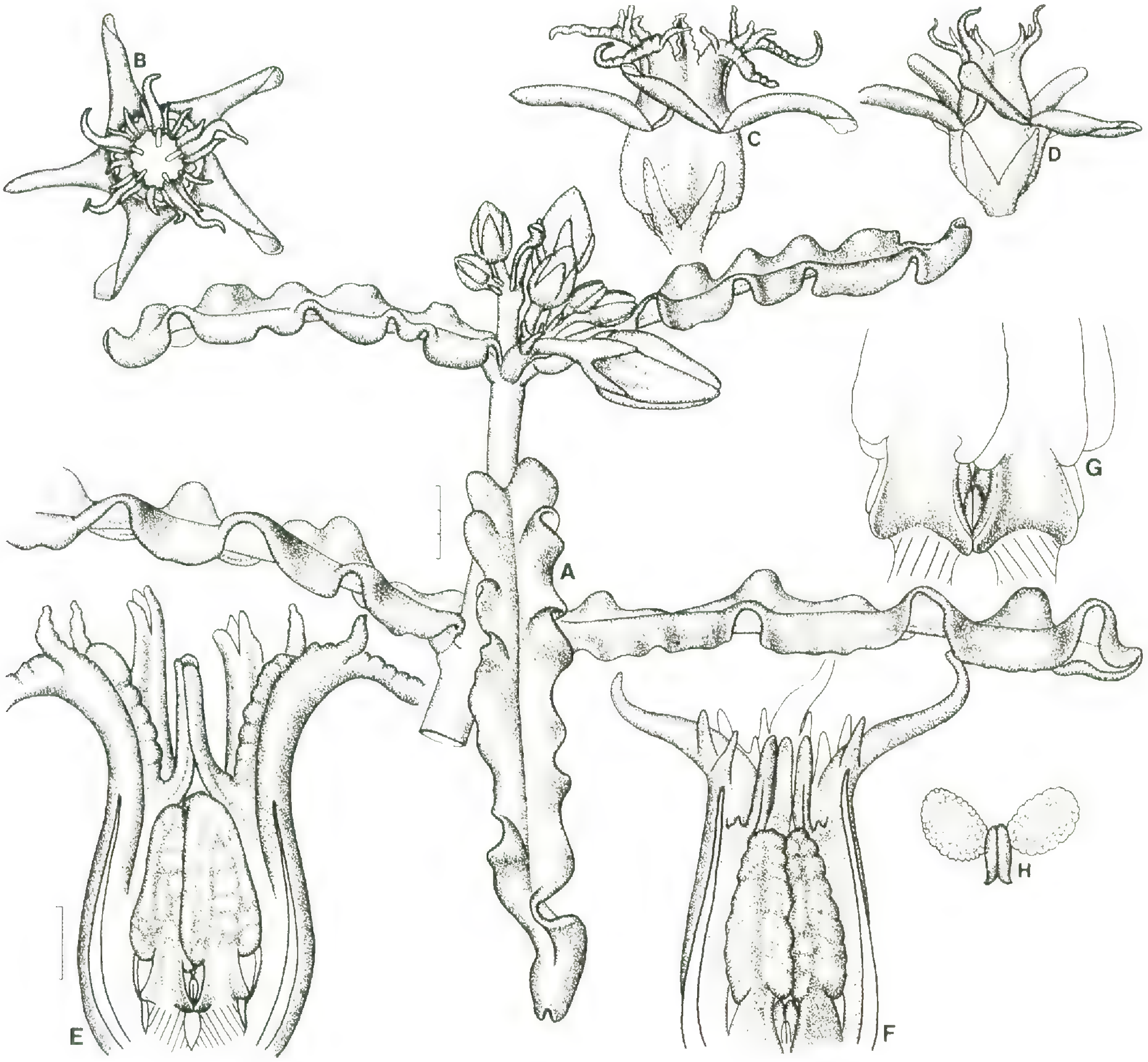

Figure 10. *Fockea sinuata.* —A. Tip of flowering branch. —B. Face view of flower. —C, D. Side view of flower. —E, F. Side view of dissected gynostegium. —G. Side view of anthers. —H. Pollinarium. Drawn from: A, B, D, H, *Bruyns 3023* (NBG); F, *Bruyns 1269* (BOL); C, E, G, *Bayer 939* (NBG). Scales: A = 3 mm; B–D = 2 mm (at A); E, F = 1 mm (at E); G = 0.5 mm (at E); H = 0.25 mm (at E).

pubescent, lower surface pubescent mainly on midrib, margins strongly undulate and revolute. *Inflorescence* 1- to 10-flowered, flowers opening in succession, covered with fine adpressed hairs; *peduncle* ca. 1 × 1 mm; *pedicels* 1–3 × 1 mm. *Sepals* 2 × 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 8–12 mm diam.; outside grayish green, sparsely pubescent; inside green to brown, sparsely pubescent; *tube* 1.5–2.5 mm deep, ca. 3 mm broad at mouth, cupular; *lobes* 3–4.5 × 2 mm, linear, obtuse, spreading, often twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming tube 4–6 mm long, becoming slightly narrower above anthers, divided at mouth of tube into 5 longer slender terete (often wrinkled) and strongly spreading lobules 2–2.5 mm long each flanked by 2 flattened erect lobules, these groups of 3 lobes alternating with 5 linear to truncate-emarginate usually erect lobules; *inner corona* of 5 terete linear lobes adpressed to backs of anthers then rising in erect column above them. *Follicles* 50–80 × 10–12 mm, gray-green, often warty; *seeds* 8–10 × 4–6 mm, yellow-brown, with hairs around margin.

Phenology. Flowering October to May.

Distribution. Namibia, South Africa: 500–1200 m (Fig. 11).

Fockea sinuata has a very scattered (and almost certainly not well-documented) distribution over the karroid parts of southern Africa from near Maltahöhe in Namibia to the Free State in South Africa and the southern portions of the Eastern Cape.

Ecology. *Fockea sinuata* is always found in open, flat, often pan-like areas and usually in loamy, slightly

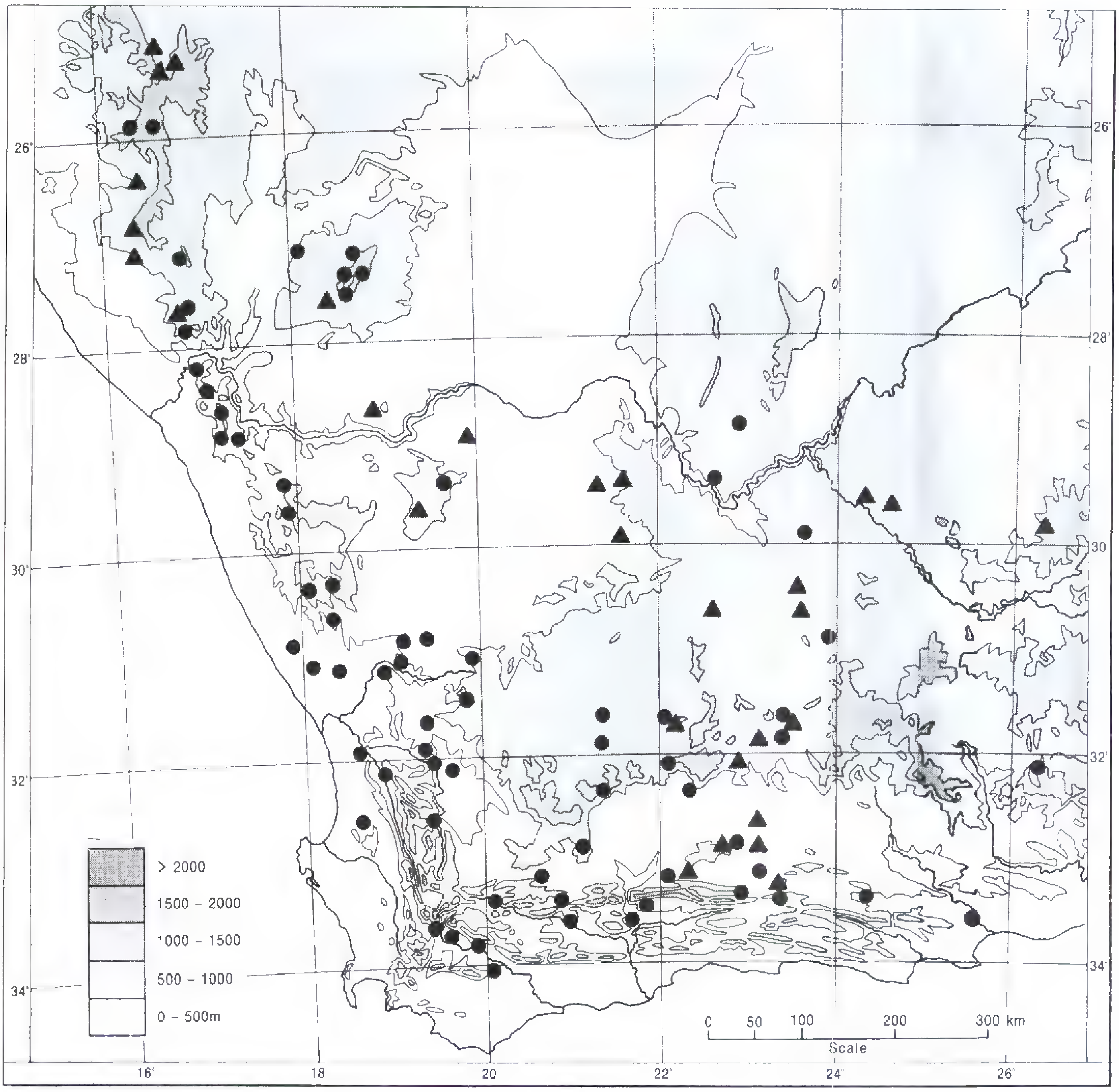

Figure 11. Map of the southwestern part of southern Africa, showing distribution of *Fockea comaru* (circles) and *Fockea sinuata* (triangles).

calcareous ground. Specimens occasionally grow among shrubs of *Rhigozum trichotomum* Burch. but more usually occur with various species of *Salsola* L. and *Zygophyllum* L. in areas of quite low diversity.

Discussion. Meyer (1838: 196) cited two specimens collected by Drège, one from "Dwyka" and the other from "Brakvalei," both without numbers. Only one, *Drège 3439B*, from Brakvallei has been located. Here we assume this to have been seen by Meyer, and it is selected as a lectotype.

In *Fockea sinuata* the plant mostly consists of only a very small erect stem 6–10 cm tall, but very occasionally the stems may twine on the lower branches of a nearby shrub. The narrow leaves have strongly undulate margins and are usually brown-green. Both of these features serve to make them exceedingly inconspicuous and lend them a strong resemblance to the stems of some of the other plants with which they grow. The leaves and some of the above-ground parts die off during the dry season. The pendulous follicles dangle down onto the ground and, in contrast to the rest of the plant, are comparatively conspicuous. In fact, the follicle may often be all that one sees of the plant, especially if the leaves are small and are not well developed.

With its mostly erect and non-twining growth and narrow leaves, *Fockea sinuata* somewhat resembles *F. comaru*. The two species never grow together, though, for *F. comaru* does not occur in low-lying places in the areas where *F. sinuata* occurs. The leaves of *F. sinuata* always have strongly undulate margins, and this is usually enough to distinguish them. Florally

they are mostly easily recognizable. In *F. sinuata* the corolla is always small, with short and twisted lobes and a comparatively large and conspicuous white corona. In some flowers the corona lobes have a pustulate inner surface, but that has not proved to be constant (Fig. 10). The pollinarium is also distinctive, with fairly swollen pollinia and a larger and darker corpuscle than in the others. The pollinium is always rather flat in *F. comaru*, and the corpuscle is also particularly slender (compare Figs. 8G and 10H).

Perhaps one of the most unusual features of *Fockea sinuata* is the fact that each seed has a row of hairs all the way around the margin (Bayer, 1976). This is a rare phenomenon that is otherwise only known in *Raphionacme namibiana* Venter & Verhoeven (Bruyns, 1994). The seedling of *F. sinuata* is also unique for its comparatively long and fleshy hypocotyl, which has always been observed to have a distinctly warty surface around the middle (Fig. 4A).

Over its extremely wide distribution within South Africa, this species is generally well known where it occurs. The tubers are often excavated and eaten, and it is locally usually known as *vlak-kambroo*.

Specimens examined. NAMIBIA. 6 km NE of Nuwerus, *Bruyns 5667* (BOL); Rooiberg Suid, *Bruyns 5670* (MO, WIND); Happy Days, *Mostert* (WIND); 62 km S of Helmeringhausen, *Mueller 58* (PRU); Kubub, *Giess et al. 5300* (M, PRE, WIND); betw. Aus and Rosh Pinah, *Mannheimer 860* (WIND); Sebrafontein, *Bruyns 3914* (BOL); Grabwasser, *Bruyns 3641* (BOL, WIND); Vrede, *Bruyns 8154* (WIND).

SOUTH AFRICA. 16 km NE of Bladgrond, *Acocks 14264* (PRE); Middeldeurvlei, *Louw* (NBG); Steenkop, *Bruyns 3459* (BOL); 30 km ENE Kenhardt, *Leistner 2325* (KMG, PRE); Diemansput-Suid, *Bruyns 3444* (BOL); Ramah, *Bayer 939* (NBG); Bulberg, *Bruyns 5121* (PRE); 25 km N of Britstown, *Bruyns 6396* (BOL); Britstown commonage, *Bruyns 3023* (NBG); Boesmansberg, Juriesfontein, *Bruyns 6689* (BOL); Bulthouersfontein, *Bruyns 5404* (BOL); 16 km N of Three Sisters, *Bruyns 5106* (BOL); Schoppelmaaikraal, *Bruyns 1269* (BOL); Renosterkop, *Burke* (K); Prutkraal, *Bayer 328* (NBG), *Snyman* (NBG); Rooidam, *Bruyns 2950* (BOL); Rietbron, *Bruyns 3133* (NBG); Tierberg, *Bruyns 3695* (BOL), *Marloth 4494* (PRE); Willowmore, *Brauns sub STE 19941* (NBG); Palmietfontein, *Smith 5344* (PRE); Rosemaryn, *Henrici 3659* (PRE).

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APPENDIX 1

THE 13 MORPHOLOGICAL CHARACTERS AND THEIR CODING AS USED IN THE ANALYSES (SEE TABLE 2 FOR ASSIGNMENT OF CHARACTER STATES TO SPECIES)

Rootstock

1. Plants without tuber = 0; with tuber = 1.
2. Upper surface of tuber flush with surface of ground = 0; well below surface of ground = 1.
3. Upper surface of tuber without warts = 0; warty = 1.

The rootstock in all species of *Fockea* other than *F. multiflora* consists of a swollen, fleshy, edible, roughly turnip-shaped stem-tuber that either projects slightly from the ground (in *F. capensis* and *F. edulis*) or is well below the surface (in *F. angustifolia*, *F. comaru*, and *F. sinuata*). The upper surface of this tuber is distinctly warty in *F. capensis* and *F. edulis* and is smooth in the others.

Stems

4. Sap milky = 0; sap clear = 1.

Leaves

5. Leaves frequently narrowly linear = 0; never linear = 1.
6. Margins of leaves strongly undulating = 0; not undulating = 1.

Very narrowly linear leaves are characteristic of *Fockea comaru* and *F. sinuata* and are also prevalent in *F. angustifolia*, where, however, they are extremely variable. The margins of the leaves are very strongly undulate in *F. sinuata* and *F. capensis*, and they are strongly revolute in *F. comaru*.

Gynostegium

7. Corolline corona absent = 0; present = 1.
8. Gynostegial corona absent = 0; present = 1.
9. Gynostegial corona of one series of lobes behind anthers only = 0; with two series of lobes = 1.
10. Outer series of gynostegial corona fused into tube = 0; not forming tube = 1.
11. Lobes of inner series of gynostegial corona long, slender, and much exceeding anthers = 0; not exceeding anthers = 1.
12. Anthers with swollen appendages filling up tube of corona = 0; without swollen appendages = 1.

Pollinarium

13. Pollinarium without caudicles = 0; with caudicles = 1.

IS *MANDEVILLA* (APOCYNACEAE, MESECHITEAE) MONOPHYLETIC? EVIDENCE FROM FIVE PLASTID DNA LOCI AND MORPHOLOGY[1]

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Abstract

In order to test the monophyly of *Mandevilla* Lindl., the largest genus in tribe Mesechiteae (Apocynaceae, Apocynoideae), and its affinities to other genera in the tribe, maximum parsimony analysis was conducted on a data set comprising DNA sequences from five plastid loci (*rpl*16, *rps*16, and *trn*K introns; *trn*S^{GCU}-*trn*G^{UUC} intergenic spacer; and *mat*K gene), as well as morphological data for 65 taxa of Mesechiteae (48 *Mandevilla*) and nine taxa from other tribes of the subfamily. *Mandevilla*, as circumscribed by Pichon, was found to be monophyletic, whereas Woodson's circumscription proved to be polyphyletic. Thus defined, *Mandevilla* forms a strongly supported clade that can be divided into six clades of species groups. Most of the infrageneric taxa of *Mandevilla* proposed by Woodson and Pichon are polyphyletic. Many of the diagnostic characters previously used to define taxonomic groups are shown to have arisen multiple times, rendering them unsuitable for classificatory purposes. The similar growth form and tubular flowers of *Macrosiphonia* Müll. Arg. and *Telosiphonia* (Woodson) Henr., two geographically disjunct segregates, represent the most extreme case of parallel evolution within *Mandevilla*, with their striking similarities most likely correlated to colonization of open, dry habitats and pollination by hawkmoths.

Key words: Apocynaceae, *Mandevilla*, *mat*K, Mesechiteae, morphology, phylogenetic systematics, *rpl*16, *rps*16, *trn*K, *trn*S^{GCU}-*trn*G^{UUC}.

Mandevilla Lindl., a member of tribe Mesechiteae, is the largest Neotropical genus in Apocynaceae and comprises about 150 species (Simões et al., 2004; Sales et al., 2006). It is distributed throughout the Neotropics, from Mexico to Argentina, in a wide variety of habitats such as deserts, savannas, tepuis, open grasslands, and forests. Morphological variation is remarkable in the genus in both vegetative and reproductive parts. Most species are vines, but erect shrubs are also common, while unbranched subshrubs and epiphytes occur less frequently. Flower size and structure are also very diverse, ranging from inconspicuous white, tubular flowers less than 1 cm long to brightly colored, showy infundibuliform flowers up to 9 cm long. The genus is traditionally characterized by the following set of traits: racemose inflorescence; leaf blade with one to many colleters on the adaxial surface, sometimes extending along the midrib; and style head with five strongly protruding, well-developed longitudinal ribs (Woodson, 1933; Pichon, 1948; Henrickson, 1996; Morales, 1998; Simões & Kinoshita, 2002; Simões et al., 2004).

A combination of high morphological diversity and broad geographic distribution makes *Mandevilla* one of the most challenging and complex genera of Neotropical Apocynaceae, a fact that is reflected in its taxonomic history. The currently accepted circumscription of *Mandevilla* was defined by Woodson in

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1933. In a broad taxonomic study of the Neotropical species of subfamily Apocynoideae, he made significant changes in the circumscription of *Mandevilla*, including in its synonymy such genera as *Exothostemon* (G. Don) Woodson, *Dipladenia* A. DC., *Laseguea* A. DC., *Amblyanthera* Müll. Arg., *Heterothrix* Müll. Arg., and part of *Echites* P. Browne. *Macrosiphonia* Müll. Arg., a small group of shrubby species with long, white, tubular flowers and a disjunct distribution in the arid zones of the southwestern U.S.A. and Mexico and the savannas of southern South America, was maintained by Woodson as a separate genus. He admitted, however, that the distinctions between *Macrosiphonia* and *Mandevilla*, based on plant habit, flowering time, and style head structure, were extremely tenuous. He also cautiously recognized two subgenera in *Macrosiphonia* (Woodson, 1933: 778), *Telosiphonia* Woodson and *Eumacrosiphonia* Woodson (= *Macrosiphonia*), comprising the species that occur in the Northern and Southern Hemispheres, respectively.

In addition to broadening the limits of *Mandevilla*, Woodson (1933) also proposed a morphologically based infrageneric classification of the genus, with the subgenera *Exothostemon* and *Eumandevilla* Woodson (= *Mandevilla*). The two subgenera were differentiated based on the following suite of morphological characters: species of subgenus *Exothostemon* have leaf colleters distributed along the entire length of the midrib, calycine colleters with an opposite arrangement, and a curved corolla tube, whereas species of subgenus *Mandevilla* have leaf colleters restricted to the base of the midrib, calycine colleters with an alternate or continuous arrangement, and a straight corolla tube.

Within subgenus *Mandevilla*, Woodson (1933) proposed a further subdivision with five sections: *Laxae* Woodson, *Montanae* Woodson, *Tenuifoliae* Woodson, *Torosae* Woodson, and *Tubiflorae* Woodson, which were differentiated based mainly on corolla shape, anther base shape, and number and size of nectaries. The largest section, *Laxae*, included 46 species distributed throughout South America and was characterized by infundibuliform corollas. Section *Montanae* consisted of 16 species also distributed in South America and was characterized by flowers with salverform to tubular-salverform corollas, anthers with a truncate base, and nectaries varying in number from two to five or even absent in some species. The smallest section, *Tenuifoliae*, comprising only two South American species, *M. myriophyllum* (Taub.) Woodson and *M. tenuifolia* (J. C. Mikan) Woodson, was distinguished from section *Montanae* by having anthers with auriculate bases and two nectaries. The two remaining sections, *Torosae* and *Tubiflorae*, have five and eight species, respectively, and are distributed in Mexico and Mesoamerica. Both of these sections were characterized by flowers with salverform to tubular-salverform corollas, anthers with auriculate bases, and five nectaries surrounding the ovary, but differed from one another in the size of the nectaries, which were said to be equal to or taller than the ovary in section *Tubiflorae* and shorter than the ovary in section *Torosae*.

A revised classification of *Mandevilla* was published by Pichon in 1948. He expanded Woodson's (1933) circumscription by including *Macrosiphonia*, which he justified by arguing that the characters used by Woodson to differentiate between the two genera were inconsistent and arbitrary. He did not consider Woodson's subgenera *Macrosiphonia* and *Telosiphonia* to be each other's closest relatives, however, and placed them in two distinct sections, based on the absence of a pedicel, longer staminal filaments, and larger pollen grains of the former. Within *Mandevilla*, Pichon recognized Woodson's subgenus *Mandevilla* and subgenus *Exothostemon* as valid groups but did not recognize his five sections within subgenus *Mandevilla*. According to Pichon, the characters supporting these two subgenera were reliable, whereas those supporting the sections were highly inconsistent, with no real diagnostic states to define them. Pichon (1948) proposed a new infrageneric classification within *Mandevilla*, recognizing four sections (*Orthocaulon* Pichon, *Exothostemon* Pichon, *Megasiphon* Pichon, and *Telosiphonia* Pichon). A summarized comparison between the infrageneric classification of Woodson (1933) and Pichon (1948) is provided in Table 1.

Since Pichon's work (1948, 1950), very few studies have investigated the taxonomy of *Mandevilla* and related genera. In 1991, Zarucchi described *Quiotania* Zarucchi as a monotypic genus morphologically very similar to *Mandevilla*, and Woodson's subgenus *Telosiphonia* was later elevated to generic status by Henrickson (1996). Another relevant work was a synopsis of the Mexican and Central American species of *Mandevilla* by Morales (1998), with new taxonomic combinations involving the species from Woodson's sections *Tubiflorae* and *Torosae*, many of these reduced to synonymy. In addition, a large number of new species of *Mandevilla* have been described in the past few decades, increasing the number of published species from the 108 recognized by Woodson in 1933 to about 150 at present. Although new information has been accumulating for the genus, no overall classification within *Mandevilla* as a whole has been proposed since Pichon (1948). Taxonomic difficulties involving both generic and infrageneric concepts have persisted for the past

Table 1. Comparison of Woodson's (1933) subgenera and sections of *Mandevilla* and their corresponding ranks in Pichon's (1948) classification.

Woodson (1933)	Pichon (1948)
Mandevilla subg. *Exothostemon*	*Mandevilla* sect. *Exothostemon*
Mandevilla subg. *Mandevilla*	*Mandevilla* sect. *Orthocaulon*
Section *Laxae*	
Section *Montanae*	
Section *Tenuifoliae*	
Section *Torosae*	
Section *Tubiflorae*	
Genus *Macrosiphonia*	
Subgenus *Macrosiphonia*	*Mandevilla* sect. *Megasiphon*
Subgenus *Telosiphonia*	*Mandevilla* sect. *Telosiphonia*

seven decades and still remain, as pointed out by Zarucchi (1991: 35): "The last word concerning generic limits of the *Mandevilla–Mesechites–Macrosiphonia* complex and near relatives has obviously not yet been written."

The use of phylogenetic methods has been successfully applied in Apocynaceae to solve controversial aspects of classification within the family. Previous studies have addressed the circumscription of Apocynaceae s. str. and their relationships with the former Asclepiadaceae (e.g., Judd et al., 1994; Sennblad & Bremer, 1996, 2002; Potgieter & Albert, 2001), but a growing number of works have focused on relationships within Apocynaceae s. str. Examples include overviews by Endress et al. (1996) and Sennblad et al. (1998) for tribe Wrightieae, a study by Endress et al. (2007) for Alyxieae, and a larger-scale study of subfamily Apocynoideae by Livshultz et al. (2007). Phylogenetic studies based on morphological characters were also published by Sidiyasa (1998) for *Alstonia* R. Br., van der Ham (2001) for Alyxieae, and Williams (2004) for *Echites*.

Simões et al. (2004) provided the first phylogenetic study of tribe Mesechiteae, with suggestions for taxonomic improvements in tribal and intergeneric delimitations. Preliminary results were obtained for *Mandevilla* and related genera, but due to the limited taxon sampling within *Mandevilla*, no firm conclusions could be drawn as to infrageneric relationships. Our present study represents the subsequent second step in interpreting the phylogeny of Mesechiteae by focusing on the intergeneric and infrageneric relationships of its largest genus, *Mandevilla*.

The aims of the present article are to test the monophyly of *Mandevilla* and determine its relationships to the putatively affined genera *Macrosiphonia*, *Telosiphonia*, and *Quiotania*, using both morphology and DNA sequence data from five chloroplast DNA loci. The resulting phylogenetic hypotheses of monophyly and infrageneric relationships of *Mandevilla* are compared with the classifications of Woodson (1933) and Pichon (1948). Morphological features consistent with the retrieved clades and/or used to define taxonomic ranks are also discussed.

Materials and Methods

Taxon Sampling

Sixty-five taxa of Mesechiteae, including representatives from all genera of the tribe recognized by Simões et al. (2004) (*Allomarkgrafia* Woodson, *Forsteronia* G. Mey., *Macrosiphonia*, *Mandevilla*, *Mesechites* Müll. Arg., *Telosiphonia*, and *Tintinnabularia* Woodson), were included in this study (Appendix 1). In order to test the infrageneric classifications of *Mandevilla* proposed by Woodson (1933) and Pichon (1948) (Table 1), 48 accessions (from 47 species) of *Mandevilla*, representing all subgenera and sections, were sampled (Table 2). Nine outgroup taxa representing all but the basalmost tribe (Wrightieae) of subfamily Apocynoideae were chosen, based largely on previous studies suggesting that the closest relatives of Mesechiteae are either Apocyneae or Echiteae (Sennblad et al., 1998; Sennblad & Bremer, 2002; Simões et al, 2004). Two genera from Echiteae (*Prestonia* R. Br. and *Rhodocalyx* Müll. Arg.) and five from Apocyneae (*Beaumontia* Wall., *Chonemorpha* G. Don, *Odontadenia* Benth., *Secondatia* A. DC., and *Trachelospermum* Lem.) were included. Two species of *Pachypodium* Lindl. (Malouetieae) were used to root the cladograms.

DNA Extraction, Amplification, and Sequencing

Total genomic DNA was extracted from silica dried leaf material or from herbarium specimens using DNeasy Plant Mini Kits (Qiagen, Valencia, California, U.S.A.) following the manufacturer's protocol. Five plastid loci (*rpl*16, *rps*16, and *trn*K introns: *trn*S^{GCU}-*trn*G^{UUC} intergenic spacer; and *mat*K gene) were amplified. Double-stranded DNA was amplified by polymerase chain reaction (PCR) on a Biometra Tgradient machine (Biometra, Göttingen, Germany), applying a thermal cycling program of 34 cycles of denaturation at 95°C for 30 seconds, annealing at 52°C for 1 minute, and extension at 72°C for 90 seconds. The *trn*K intron and *mat*K gene were co-amplified in a single PCR reaction, and the thermal cycling program was modified in the following steps: denaturation at 94°C for 30 seconds and annealing at 54°C for 1 minute. For some taxa, amplification of the entire *trn*K intron/*mat*K locus

Table 2. List of the sampled taxa of *Macrosiphonia*, *Mandevilla*, and *Telosiphonia* and their placement in the classification of Woodson (1933) and the clades observed in the present study.

Taxon name and current classification	This study
Genus *Macrosiphonia* Müll. Arg.	
Macrosiphonia longiflora (Desf.) Müll. Arg.	Clade I
Macrosiphonia martii Müll. Arg.	Clade I
Macrosiphonia velame (A. St.-Hil.) Müll. Arg.	Clade I
Genus *Mandevilla* Lindl.	
Subgenus *Mandevilla* Woodson, as "*Eumandevilla*"	
Section *Laxae* Woodson	
Mandevilla atroviolacea (Stadelm.) Woodson	Clade III
Mandevilla callista Woodson	Clade I
Mandevilla coccinea (Hook. & Arn.) Woodson	Clade III
Mandevilla convolvulacea (A. DC.) Hemsl.	Clade IV
Mandevilla duartei Markgr.	Clade III
Mandevilla fragrans (Stadelm.) Woodson	Clade III
Mandevilla funiformis (Vell.) K. Schum.	Clade I
Mandevilla glandulosa (Ruiz & Pav.) Woodson	Clade IV
Mandevilla harleyi M. F. Sales, Kin.-Gouv. & A. O. Simões	Clade I
Mandevilla illustris (Vell.) Woodson	Clade III
Mandevilla laxa (Ruiz & Pav.) Woodson	Clade IV
Mandevilla ligustriflora Woodson	Clade IV
Mandevilla martiana (Stadelm.) Woodson	Clade III
Mandevilla moricandiana (A. DC.) Woodson	Clade III
Mandevilla oaxacana (A. DC.) Hemsl.	Clade IV
Mandevilla pendula (Ule) Woodson	Clade III
Mandevilla pohliana (Stadelm.) A. H. Gentry	Clade III
Mandevilla sancta (Stadelm.) Woodson	Clade III
Mandevilla sellowii (Müll. Arg.) Woodson	Clade III
Mandevilla spigeliiflora (Stadelm.) Woodson	Clade III
Mandevilla splendens (Hook. f.) Woodson	Clade III
Mandevilla urophylla (Hook. f.) Woodson	Clade III
Mandevilla venulosa (Müll. Arg.) Woodson	Clade III
Mandevilla veraguasensis (Seem.) Hemsl.	Clade IV
Section *Montanae* Woodson	
Mandevilla cercophylla Woodson	Clade IV
Mandevilla emarginata (Vell.) C. Ezcurra	Clade IV
Mandevilla jamesonii Woodson	Clade IV
Mandevilla pentlandiana (A. DC.) Woodson	Clade IV
Mandevilla pycnantha (Steud. ex A. DC.) Woodson	Clade III
Mandevilla tricolor Woodson	Clade IV
Section *Tenuifoliae* Woodson	
Mandevilla myriophyllum (Taub.) Woodson	Clade III
Mandevilla tenuifolia (J. C. Mikan) Woodson	Clade III
Section *Torosae* Woodson	
Mandevilla foliosa (Müll. Arg.) Hemsl.	Clade IV
Mandevilla karwinskii (Müll. Arg.) Hemsl.	Clade IV
Section *Tubiflorae* Woodson	
Mandevilla syrinx Woodson	Clade IV
Mandevilla tubiflora (M. Martens & Galeotti) Woodson	Clade IV
Subgenus *Exothostemon* (G. Don) Woodson	
Mandevilla anceps Woodson	Clade I
Mandevilla dodsonii A. H. Gentry	Clade I
Mandevilla hirsuta (Rich.) K. Schum.	Clade I
Mandevilla krukovii Woodson	Clade I
Mandevilla lancifolia Woodson	Clade I
Mandevilla leptophylla (A. DC.) K. Schum.	Clade I
Mandevilla nerioides Woodson	Clade I

Table 2. Continued.

Taxon name and current classification	This study
Mandevilla rugellosa (Rich.) L. Allorge	Clade I
Mandevilla rugosa (Benth.) Woodson	Clade I
Mandevilla scabra (Hoffmanns. ex Roem. & Schult.) K. Schum.	Clade I
Mandevilla subsagittata (Ruiz & Pav.) Woodson	Clade I
Genus *Telosiphonia* (Woodson) Henr.	
Telosiphonia brachysiphon (Torr.) Henr.	Clade IV
Telosiphonia hypoleuca (Benth.) Henr.	Clade IV
Telosiphonia nacalpulensis Felger & Henr.	Clade IV

was only possible by fragmenting that region into two parts, using a combination of external and internal primers. Reactions were terminated with a final extension of 4 minutes at 72°C for the *rpl16* intron, *rps16* intron, and *trn*S^{GCU}-*trn*G^{UUC} spacer, and 7 minutes for the *trn*K intron and *mat*K gene. All PCR reactions were performed in a total volume of 25 μL, using 2.5 mM $MgCl_2$ 10× PCR* buffer (Amersham Biosciences, Piscataway, New Jersey, U.S.A.), 0.25 mM of dNTP, 0.5 units of Taq DNA polymerase (Amersham Biosciences, lot 17544), 1 to 4 μl of bovine serum albumin (BSA; Sigma, Steinheim, Germany), and 0.1 mM of each primer.

Primer information is presented in Table 3. For some taxa, internal primers were also used to amplify the *rpl*16 intron and *trn*S^{GCU}-*trn*G^{UUC} intergenic spacer, with the following changes in the thermal cycling program: 40 instead of 34 cycles and extension time shortened to 1 minute. Successfully amplified PCR products were then purified using GFX PCR DNA and Gel Band Purification Kit (Amersham Biosciences).

For some taxa with DNA extracted from herbarium vouchers, no amplified products were obtained with our initial PCR protocols and primer sets. In those cases, amplification was only successful using a two-step amplification procedure. A first round of PCR amplification was performed using the total genomic DNA as a template, followed by a second round using one external and one internal primer and a 10% dilution of the product of the first amplification as a template. The two-round amplification procedure was used to obtain products of the *trn*K intron and *mat*K gene for six species (*Mandevilla anceps* Woodson, *M. krukovii* Woodson, *M. lancifolia* Woodson, *M. leptophylla* (A. DC.) K. Schum., *M. nerioides* Woodson, *M. tricolor* Woodson, and *Tintinnabularia mortonii* Woodson).

Cycle-sequencing reactions were carried out using an ABI Prism Big Dye Terminator Cycle Sequencing Ready Extraction Kit (Perkin Elmer, Applied Biosystems, Applera Europe BV, Rotkreuz, Switzerland). Sequence products were purified on MicroSpin G-50 columns (Amersham Pharmacia Biotech Europe, Dübendorf, Switzerland) and loaded on an ABI Prism 377 DNA sequencer (Perkin Elmer). Complementary strands were edited and assembled with Sequencher 3.1.1 (Gene Codes, Ann Arbor, Michigan, U.S.A.).

DATA MATRIX COMPOSITION AND PARSIMONY ANALYSES

Nucleotide sequences of the studied plastid loci were aligned using Clustal W version 1.8 (Thompson et al., 1994) and adjusted visually. Regions of mononucleotide repeats with variable length between taxa, as well as those composed of nested gaps resulting from ambiguous alignment, were excluded from the analysis. Aligned gaps were manually coded as presence/absence characters by applying the single indel coding method described by Simmons and Ochoterena (2000) for the *mat*K gene and by using the software Gapcoder (Young & Healy, 2003) for the other loci. All coded gaps were then added to the sequence matrix and used in further analyses.

Thirty-two morphological characters were coded using a combination of herbarium and fresh specimens, pickled flowers, and, when available, flower sections prepared by the second author. For some taxa, the literature was also consulted (e.g., Woodson, 1933; Pichon, 1950; Leeuwenberg, 1997; Morales, 1996, 1997, 1998). The morphological matrix and the characters and character states, including some explanatory notes on characters, are given in Appendices 2 and 3, respectively.

A total of six data sets were subjected to phylogenetic analysis, corresponding to the five loci sequenced plus morphology. Because simultaneous analysis of combined data sets has been proposed as the best approach to phylogenetic inference (Nixon & Carpenter, 1996), we tested the combinability of all partitions by searching for incongruence between individual data sets. For this, we compared the results on a node-to-node basis of all individual data sets with respect to levels of resolution and bootstrap support (BS), as applied by other authors (e.g., Wiens, 1998;

Table 3. DNA sequences of the primers used for amplification and sequencing of the five plastid loci used in this study. Primers designed for the two-step amplification are indicated by an asterisk (*).

cpDNA locus		Primers	Primer source
*rpl*16 intron	F71	5′-GCTATGCTTAGTGTGTGACTCGTTG-3′	Baum & Wendel, 1998
	R1516	5′-CCCTTCATTCTTCCTCTATGTTG-3′	Baum & Wendel, 1998
	513F	5′-GGGAACGATGGAAGCTGTGAATGC-3′	Simões et al., 2004
	542R	5′-CGCGGGCGAATATTTACTCTTC-3′	Simões et al., 2004
	*F73	5′-CYCATTACTTCGCATTATCTC-3′	This study
	*1R582	5′-CGACCAGTGAATCATTAAGAT-3′	This study
	*IF479	5′-ACAAATTTCATTATGAGCTCC-3′	This study
	*R1060	5′-GCGAATAAAAGAATTMAAA-3′	This study
rps 16 intron	*rps*F	5′-TGGTAGAAAGCAACGTGCGACTT-3′	Oxelman et al., 1997
	*rps*R2	5′-TCGGGATCGAACATCAATTGCAAG-3′	Oxelman et al., 1997
	387F	5′-CACCGAAGTAATGCCTAAACC-3′	Simões et al., 2004
	497R	5′-GGATTCTKAAGTCTGGCCCAG-3′	Simões et al., 2004
	*IF486	5′-WAACTGGGCCAGACTTMAGAA-3′	This study
	*R768	5′-CGAATAAATTACATAAAAGG-3′	This study
	*R782	5′-ATGGAATTCGAATAAATTACA-3′	This study
*trn*S^{GCU}-*trn*G^{UUC} spacer	*trn*S	5′-GCCGCTTTAGTCCACTCAGC-3′	Hamilton, 1999
	*trn*G	5′-GAACGAATCACACTTTTACCAC-3′	Hamilton, 1999
	309F	5′-GATGATTTTTCATTTATMTGA-3′	Simões et al., 2004
	527R	5′-GTGCTWAAATATTTCYYATTMAC-3′	Simões et al., 2004
*trn*K intron + *mat*K gene	*trn*K 3914F	5′-GGGGTTGCTAACTCAACGG-3′	Civeyrel & Rowe, 2001
	*mat*K 8F	5′-AATTTCAAATGGAAGAAATC-3′	Civeyrel & Rowe, 2001
	*mat*K 174R	5′-CGAKTAATTAAMCGTTTCAC-3′	Civeyrel & Rowe, 2001
	*mat*K 8F	5′-AATTTCAAATGGAAGAAATC-3′	Civeyrel & Rowe, 2001
	*mat*K 503R	5′-GCATCTTTTACCCAATAGCG-3′	Civeyrel & Rowe, 2001
	*mat*K 503F	5′-TCGCTATTGGGTAAAAGATGC-3′	Civeyrel & Rowe, 2001
	*mat*K 681F	5′-GTGAATACGAATCYATTTTC-3′	Civeyrel & Rowe, 2001
	*mat*K 900F	5′-TGGAAATTTTACCTTGTCAA-3′	Civeyrel & Rowe, 2001
	*mat*K 1628R	5′-CATGCTACATCAACATTTCAG-3′	Civeyrel & Rowe, 2001
	*mat*K 1309F	5′-GACTTTCTTGTGCTAGAACT-3′	Civeyrel & Rowe, 2001
	*trn*K 2R	5′-AACTAGTCGGATGGAGTA-3′	Civeyrel & Rowe, 2001

Sheahan & Chase, 2000; Whitten et al., 2000; Reeves et al., 2001). Because the trees generated from the individual data sets did not show any topological conflict when supported by bootstrap values greater than 75%, data partitions were then combined as follows: all molecular data sets combined (molecular combined) and all molecular data sets combined with morphology (total evidence).

Maximum parsimony analyses were performed using PAUP* 4.0b (Swofford, 2000). All characters were unordered and equally weighted. Polymorphisms in the data matrix were treated as such, rather than as uncertainties. A heuristic search for most parsimonious trees (MPT) included (1) an initial round of tree searches with 1000 random addition sequence replicates (RASR), holding 10 trees at each step, and (2) tree bisection-reconnection (TBR) branch swapping with MULTREES and steepest descent in effect, saving a maximum of 50 trees at each replicate. All shortest trees retained in the memory were then included in a second round of searches involving exhaustive TBR branch swapping. Relative support for each node was estimated using the bootstrap resampling procedure (Felsenstein, 1985) as implemented in PAUP, employing a heuristic search with 500 replicates, 250 RASR with three trees held at each step, and TBR branch swapping with steepest descent and MULTREES in effect, saving 10 trees at each RASR.

Morphological characters were mapped onto the two most parsimonious trees resulting from the total evidence analysis using MacClade 4.0 (Maddison & Maddison, 2000) in order to identify the synapomorphies that are congruent with each of the major clades of *Mandevilla* retrieved in our analyses. Unambiguous changes were then reconstructed with maximum parsimony applying both accelerated (ACCTRAN) and delayed (DELTRAN) character state optimizations.

Results

Amplification of the five selected loci was routine for most taxa. The two-round amplification of the *trn*K/*mat*K locus was only partially successful for *Mande-*

Table 4. Summary of sequence characteristics and tree statistics for separate and combined data sets. Tree length, consistency index (CI), and retention index (RI) were calculated based on parsimony-informative characters only.

	*rpl*16 Intron	*rps*16 Intron	*trn*S^{GCU}-*trn*G^{UUC} Intergenic spacer	*trn*K Intron	*mat*K Gene	Molecular combined	Morphology	Total evidence
Aligned length	1554	931	1275	1110	1554	6344	32	6376
Range of sequence length	908–1092	789–830	437–801	903–1005	1497–1554	NA	NA	NA
No. of coded gaps	212	131	177	20	6	546	NA	546
No. of characters excluded (nucleotides + gaps)	62	21	63	19	NA	165	NA	165
Total no. of parsimony-informative characters (% of total no. of characters)	242 (13.7%)	127 (12%)	127 (8.8%)	149 (13.3%)	216 (13.9%)	858 (12.5%)	32 (100%)	893 (12.9%)
Tree length	460	283	305	273	430	1653	117	1796
CI	0.521	0.551	0.475	0.667	0.644	0.619	0.205	0.594
RI	0.777	0.825	0.756	0.862	0.865	0.848	0.412	0.836

villa anceps, *M. leptophylla*, and *Tintinnabularia mortonii* and failed completely for *M. krukovii*, *M. nerioides*, and *M. tricolor*.

Multiple sequence alignment for the *mat*K gene required only a few gaps that, without exception, occurred in multiples of three. Alignment was also unproblematic for the *trn*K and *rps*16 introns but proved to be somewhat more difficult for the *rpl*16 intron and *trn*S^{GCU}-*trn*G^{UUC} spacer due to the larger number of gaps and mononucleotide repeats. A total of 165 characters, including nucleotides and gaps, were thus excluded from further analyses of the noncoding loci, mainly from the *rpl*16 intron. Manual verification of the coded gap characters showed that Gapcoder performed well, even in cases of overlapping gaps with different start and/or ending positions, and no further adjustments in the matrices were necessary. More detailed information for the individual and combined data sets is given in Table 4.

PARSIMONY ANALYSES

Tree length, consistency index (CI), and retention index (RI) for the cladograms resulting from the analyses of the individual and combined data sets are summarized in Table 4. From the individual molecular data sets, the best-resolved cladogram was provided by the *mat*K gene, with most of the nodes receiving greater than 50% BS (Fig. 1). The highest proportion of parsimony informative characters, as well as the highest CI and RI values, were also provided by this data set. Of the other data sets, the *trn*K intron (Fig. 1) and *rpl*16 and *rps*16 introns (Fig. 2) had similar levels of resolution; the least resolved cladogram was provided by *trn*S^{GCU}-*trn*G^{UUC} intergenic spacer, with the lowest number of nodes supported by at least 50% BS (Fig. 3). Of these cladograms, only the *mat*K and *trn*S^{GCU}-*trn*G^{UUC} trees defined a clade containing all species of *Mandevilla*, *Macrosiphonia*, and *Telosiphonia* with BS higher than 50%. Because no strongly supported (> 75%) incongruent clades were found between individual partitions, all molecular data sets were combined. Their analyses yielded the tree shown in Figure 4.

Analysis of the morphological data set resulted in a poorly resolved cladogram with only a few groups supported by a BS value higher than 50% (Fig. 3). No incongruent clades with BS greater than 75% were detected when comparing the morphological tree with either the strict consensus of the individual or combined molecular trees. Therefore, the morphological and combined molecular data sets were combined to form a total evidence data set.

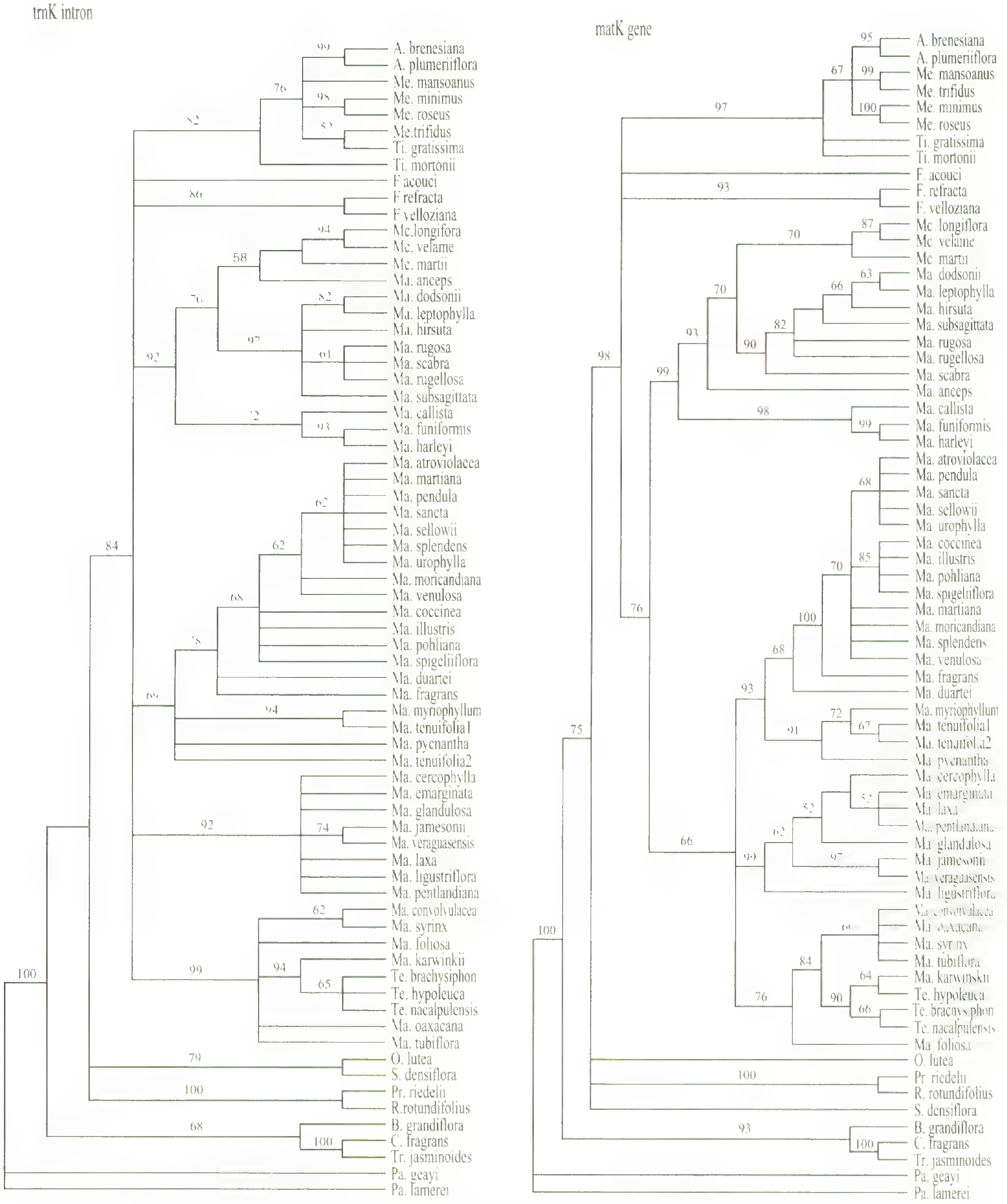

Figure 1. Strict consensus of the most parsimonious trees generated by the *trn*K intron and *mat*K gene data sets. Bootstrap values > 50% are indicated above the branches. Full taxon names are given in Appendix 1.

The total evidence tree (Fig. 5) contains a strongly supported clade (BS = 100%) including representatives of *Allomarkgrafia*, *Forsteronia*, *Macrosiphonia*, *Mandevilla*, *Mesechites*, and *Tintinnabularia* (the Mesechiteae clade). Within this clade, three strongly supported clades were recovered: (1) the *Mesechites* clade (BS = 100%), comprising *Allomarkgrafia*, *Mesechites*, and *Tintinnabularia*; (2) the *Forsteronia* clade (BS = 99%), formed by the three sampled species of this genus; and (3) the *Mandevilla* clade (BS = 94%), comprising species of *Macrosiphonia*, *Mandevilla*, and *Telosiphonia*, a result that is consistent with our earlier findings (Simões et al., 2004).

Within the *Mandevilla* clade, two major, strongly supported clades (Fig. 5; BS = 100%) were recovered: (1) one formed by *Macrosiphonia*, 11 species of *Mandevilla* subg. *Exothostemon*, and three species

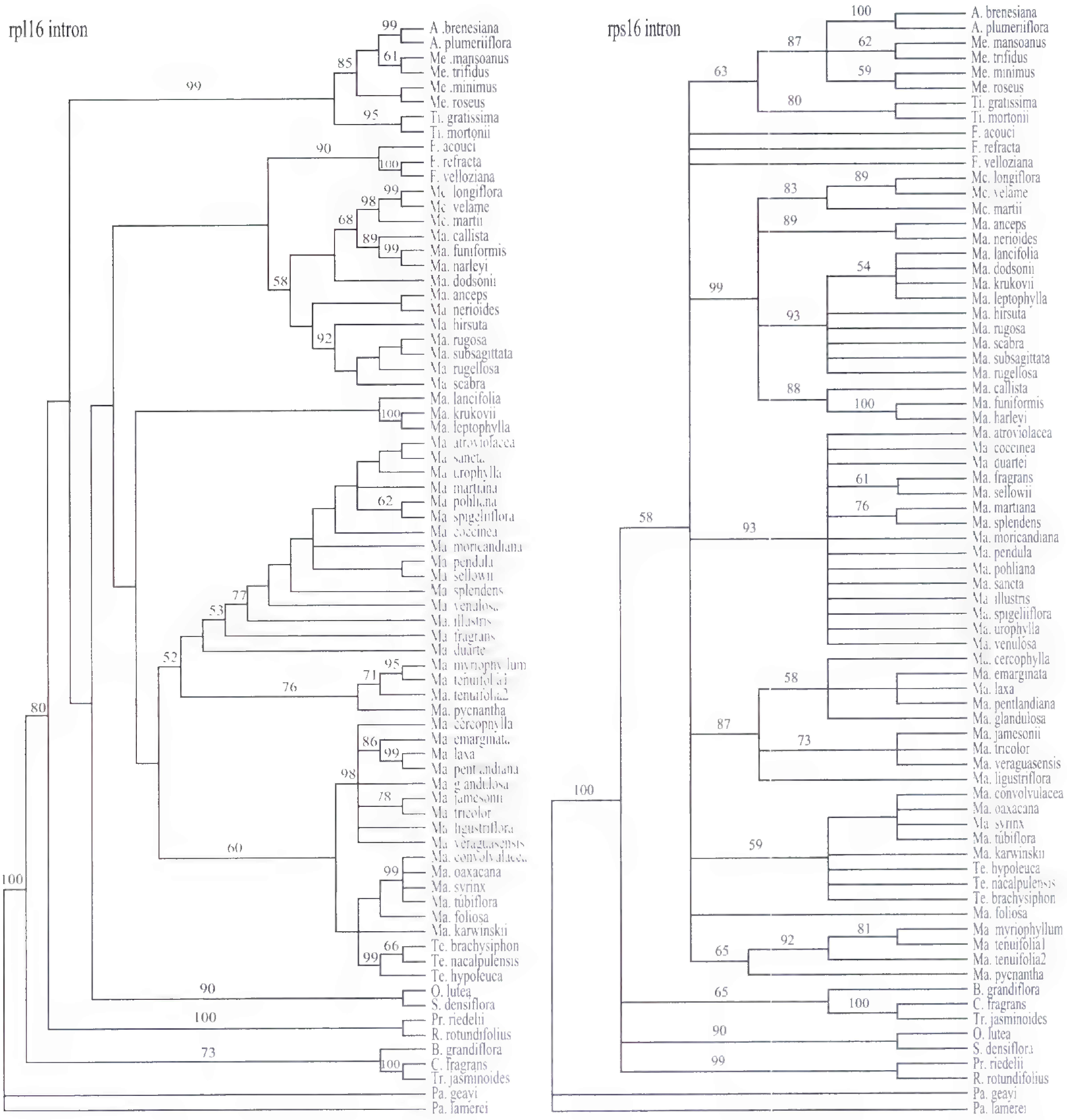

Figure 2. Strict consensus of the most parsimonious trees generated by the *rpl*16 intron and *rps*16 intron data sets. Bootstrap values > 50% are indicated above the branches. Full taxon names are given in Appendix 1.

of subgenus *Mandevilla* (*M. callista* Woodson, *M. funiformis* (Vell.) K. Schum., and *M. harleyi* M. F. Sales, Kin.-Gouv. & A. O. Simões), hereafter referred to as Clade I, and (2) another formed by *Telosiphonia* and all remaining species of *Mandevilla* sampled, hereafter referred to as Clade II.

Within Clade II, which is more morphologically diverse than Clade I and more extensively sampled in our study, two strongly supported clades were recovered: (1) a clade comprised of species of *Mandevilla* mostly from central to southern South America, hereafter referred to as Clade III, and (2) a clade consisting of *Telosiphonia* and species of *Mandevilla* with a wide range of distribution from Mexico to southern South America, hereafter referred to as Clade IV. Clade IV can, in turn, be subdivided into two smaller clades: (1) Clade V, a heterogeneous assemblage composed of the South American species of *Mandevilla* with truncate anther bases, and (2) Clade VI, formed by *Telosiphonia* and all Mexican species of *Mandevilla*.

Mapping morphological characters onto the *Mandevilla* clade shows that Clades I, IV, and V are supported by unambiguous changes in character state (Fig. 6). In Clade I, opposite calycine colleters are derived from colleters with an alternate to continuous arrangement (character no. 15, Fig. 6), with a reversal to the ancestral state in the subclade formed by

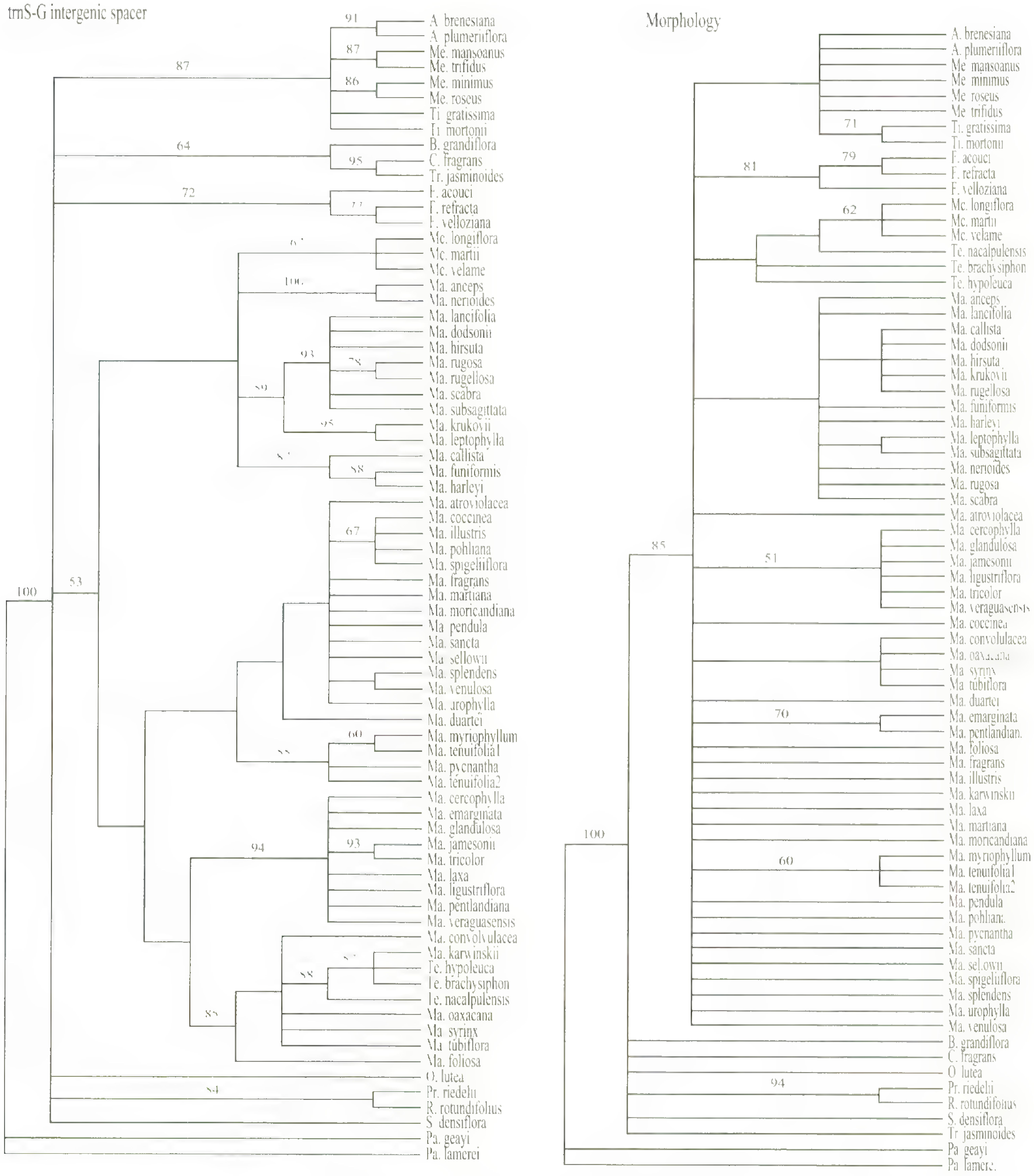

Figure 3. Strict consensus of the most parsimonious trees generated by the $trnS^{GCU}$-$trnG^{UUC}$ intergenic spacer and morphological data sets. Bootstrap values ≥ 50% are indicated above the branches. Full taxon names are given in Appendix 1.

species of *Macrosiphonia*. In Clade IV, a shift from short to long style head appendages was noted on all terminal branches, except in the subclade formed by species of *Telosiphonia* (character no. 29, Fig. 6). In Clade V, anthers with a truncate base evolved unambiguously from the ancestral state of a cordate base (character no. 20, Fig. 6). No unequivocal morphological synapomorphies were found to support Clades II, III, and IV, as ACCTRAN and DELTRAN optimizations resulted in different reconstructions of character state changes (Fig. 6). A more detailed explanation of morphological characters and changes of state is given in the discussion of each individual clade.

Discussion

Phylogenetic hypothesis and current classifications

In our study, the clade formed by species of *Mandevilla*, *Macrosiphonia*, and *Telosiphonia* (*Mandevilla* clade) largely corresponds to the circumscrip-

Molecular combined

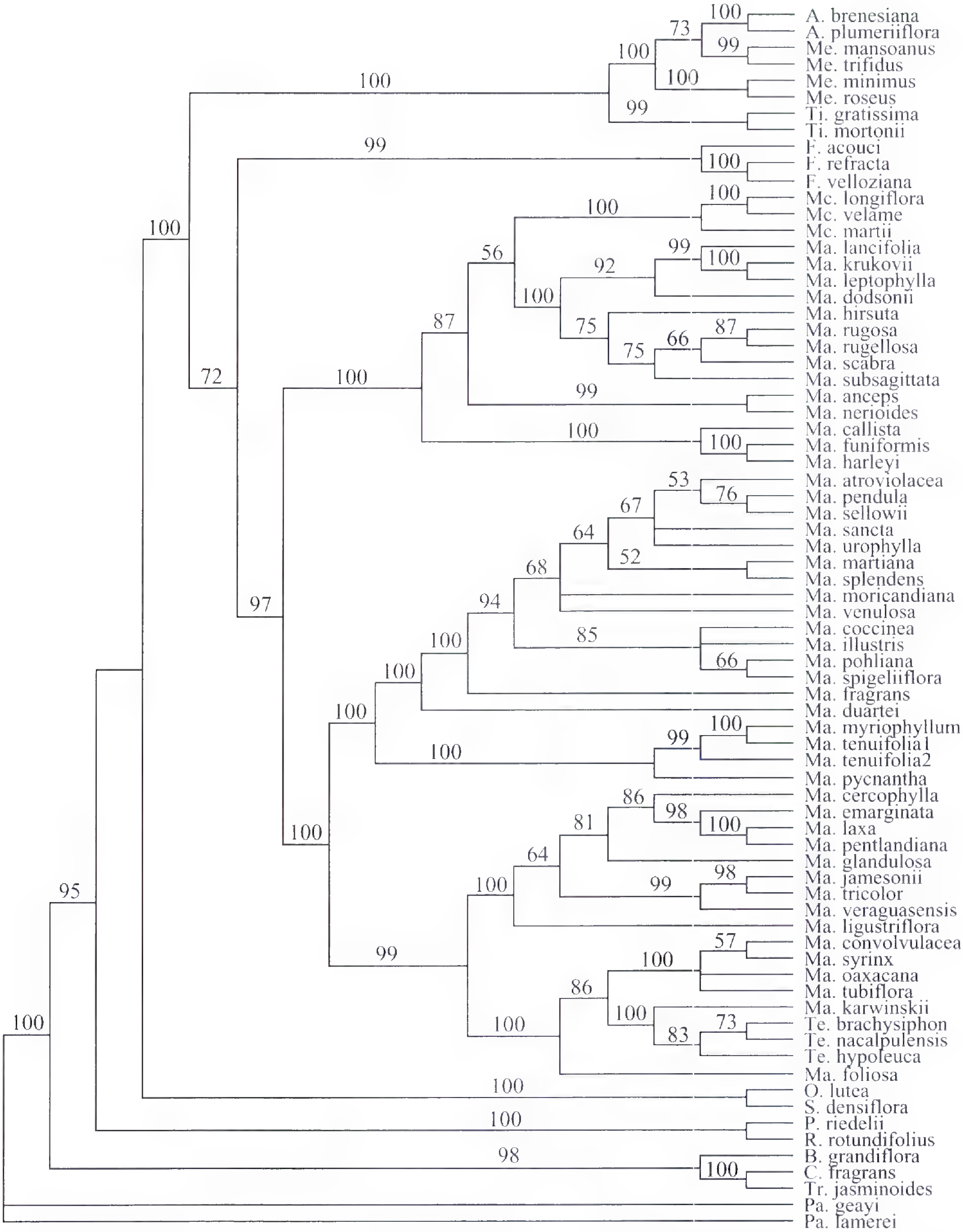

Figure 4. Strict consensus of the most parsimonious trees generated by the molecular combined data set. Bootstrap values > 50% are indicated above the branches. Full taxon names are given in Appendix 1.

tion of *Mandevilla* proposed by Pichon (1948) but only partially corresponds to that of Woodson (1933). The main difference between the two classifications concerns the rank of *Macrosiphonia* and *Telosiphonia*. Woodson (1933) recognized *Macrosiphonia* as a distinct genus with two disjunct subgenera, subgenus *Macrosiphonia* in the Southern Hemisphere and subgenus *Telosiphonia* in the Northern Hemisphere. Pichon (1948), in contrast, included *Macrosiphonia* in the synonymy of *Mandevilla*. He cited a set of

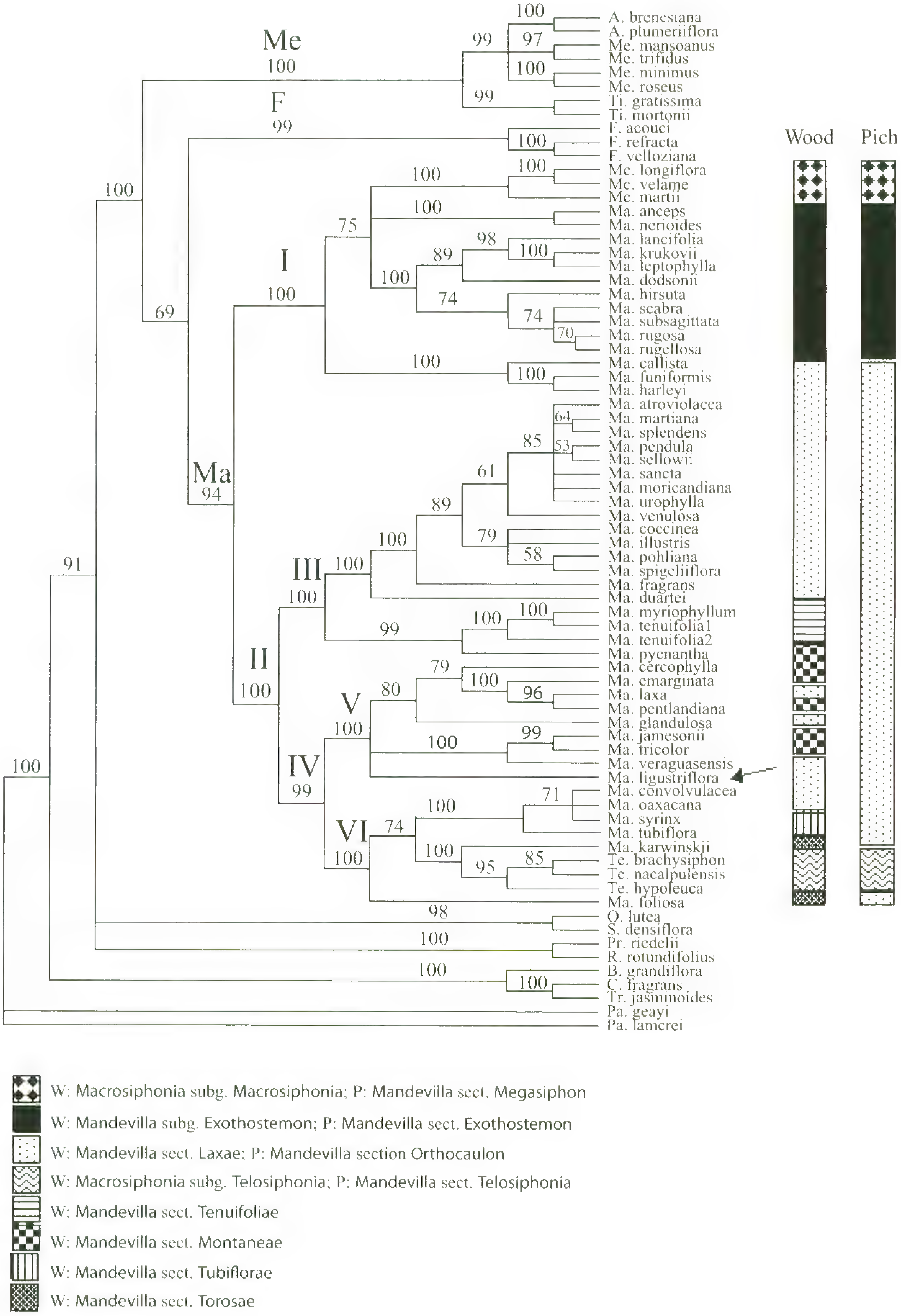

Figure 5. Strict consensus of the most parsimonious trees generated by the total evidence data set. Bootstrap values > 50% are indicated above the branches. Ma = *Mandevilla* clade; Me = *Mesechites* clade; F = *Forsteronia* clade. The six

morphological characters to differentiate between Woodson's subgenus *Macrosiphonia* and subgenus *Telosiphonia* (presence vs. absence of a pedicel, structure of staminal filaments, and pollen size) and recognized them as two different sections of *Mandevilla*, section *Megasiphon* and section *Telosiphonia*, respectively. Our results suggest that *Telosiphonia* and *Macrosiphonia* are not closely related to each other, although both are clearly nested within *Mandevilla*, and confirm the preliminary results from our previous study (Simões et al., 2004).

Most of the infrageneric groups of *Mandevilla* proposed by Woodson (1933) are not monophyletic. The two subgenera he proposed, subgenus *Exothostemon* and subgenus *Mandevilla*, correspond for the most part to the two major clades within *Mandevilla* identified in our analyses, Clades I and II, respectively (Fig. 5). To render Woodson's subgenera monophyletic, the following new classifications must be made: (1) *Macrosiphonia* must be included in subgenus *Exothostemon*, (2) *Telosiphonia* must be included in subgenus *Mandevilla*, and (3) *Mandevilla callista*, *M. funiformis*, and *M. harleyi* must be transferred from subgenus *Mandevilla* to subgenus *Exothostemon*. Of the five sections of subgenus *Mandevilla* proposed by Woodson (1933), only the smallest, section *Tenuifoliae*, containing two species, constitutes a monophyletic group (BS = 100%) in our study. All of the other sections are polyphyletic, with their constituent taxa scattered throughout the *Mandevilla* clade (Fig. 5). The most extreme case of polyphyly is found in Woodson's section *Laxae*, the largest of subgenus *Mandevilla*, which he characterized by having infundibuliform corollas. In our study, the 24 species sampled from this section are scattered among all larger subclades of the *Mandevilla* clade (Fig. 5, Table 2).

With regard to the infrageneric ranks proposed by Pichon (1948), our results support the monophyly of two of his sections, namely, *Megasiphon* and *Telosiphonia*. His other sections, *Orthocaulon* and *Exothostemon*, correspond to Woodson's subgenus *Mandevilla* and subgenus *Exothostemon*, respectively, and do not constitute monophyletic groups as indicated above. Despite their strongly supported monophyly, recognition of sections *Megasiphon* and *Telosiphonia* is untenable both taxonomically and morphologically, due to the considerable number of additional sections without morphological synapomorphies that would need to be recognized in *Mandevilla*. The same justification can be applied for not recognizing Woodson's section *Tenuifoliae*, despite its monophyly.

After a detailed examination of herbarium vouchers and phototypes, we have concluded that *Mandevilla ligustriflora* Woodson and *Quiotania colombiana* Zarucchi are conspecific. As *Q. colombiana* is the only described species of the genus and *M. ligustriflora* is nested within Clade IV with a strong bootstrap support (see Fig. 5), *Quiotania* cannot be recognized as a valid genus and should, therefore, be included in the synonymy of *Mandevilla*. The required nomenclatural changes have been undertaken in a separate paper (Simões et al, 2007).

CLADE I

Clade I contains representatives from three disparate taxonomic groups of Woodson's (1933) classification. Of the 17 species included in this clade, the majority (11) belong to Woodson's subgenus *Exothostemon*. All 11 sampled species of *Exothostemon* in our study are within this clade. Of the six remaining taxa, three (*Macrosiphonia longiflora* (Desf.) Müll. Arg., *M. martii* Müll. Arg., and *M. velame* (A. St.-Hil.) Müll. Arg.) belong to Woodson's genus *Macrosiphonia*, and the other three (*Mandevilla callista*, *M. funiformis*, and *M. harleyi*) fall under the circumscription of his subgenus *Mandevilla*. Clade I is characterized by one morphological synapomorphy: the calycine colleters have an opposite arrangement in relation to the calyx lobes (character no. 15, Fig. 6; see Appendix 3).

Subgenus *Exothostemon* forms a morphologically distinctive group within *Mandevilla*. Flower structure is quite homogeneous, with the presence of three character states considered by both Woodson (1933) and Pichon (1948) as diagnostic for the group: (1) leaf surface with many colleters distributed along the midrib on the adaxial surface; (2) opposite calycine colleters; and (3) corolla lower tube more or less gibbous or arcuate. Variation in vegetative characters and geographic distribution is, however, remarkable in the subgenus, and groups within Clade I can be discerned based on morphology. The first group, represented in our study by eight species (*M. dodsonii* A. H. Gentry, *M. hirsuta* (Rich.) K. Schum., *M. krukovii*, *M. leptophylla*, *M. rugellosa* (Rich.) L. Allorge, *M. rugosa* (Benth.) Woodson, *M. scabra*

←

subclades within the *Mandevilla* clade are indicated as I, II, III, IV, V, and VI. The arrow indicates the position of *Mandevilla ligustriflora*, which is conspecific with *Quiotania colombiana*. A comparison between the classifications of Woodson (1933) and Pichon (1948) is illustrated in the two columns on the right of the cladogram. Each pattern of the columns is associated to its corresponding taxonomic rank in Woodson's (W) and Pichon's (P) classification. Full taxon names are given in Appendix 1.

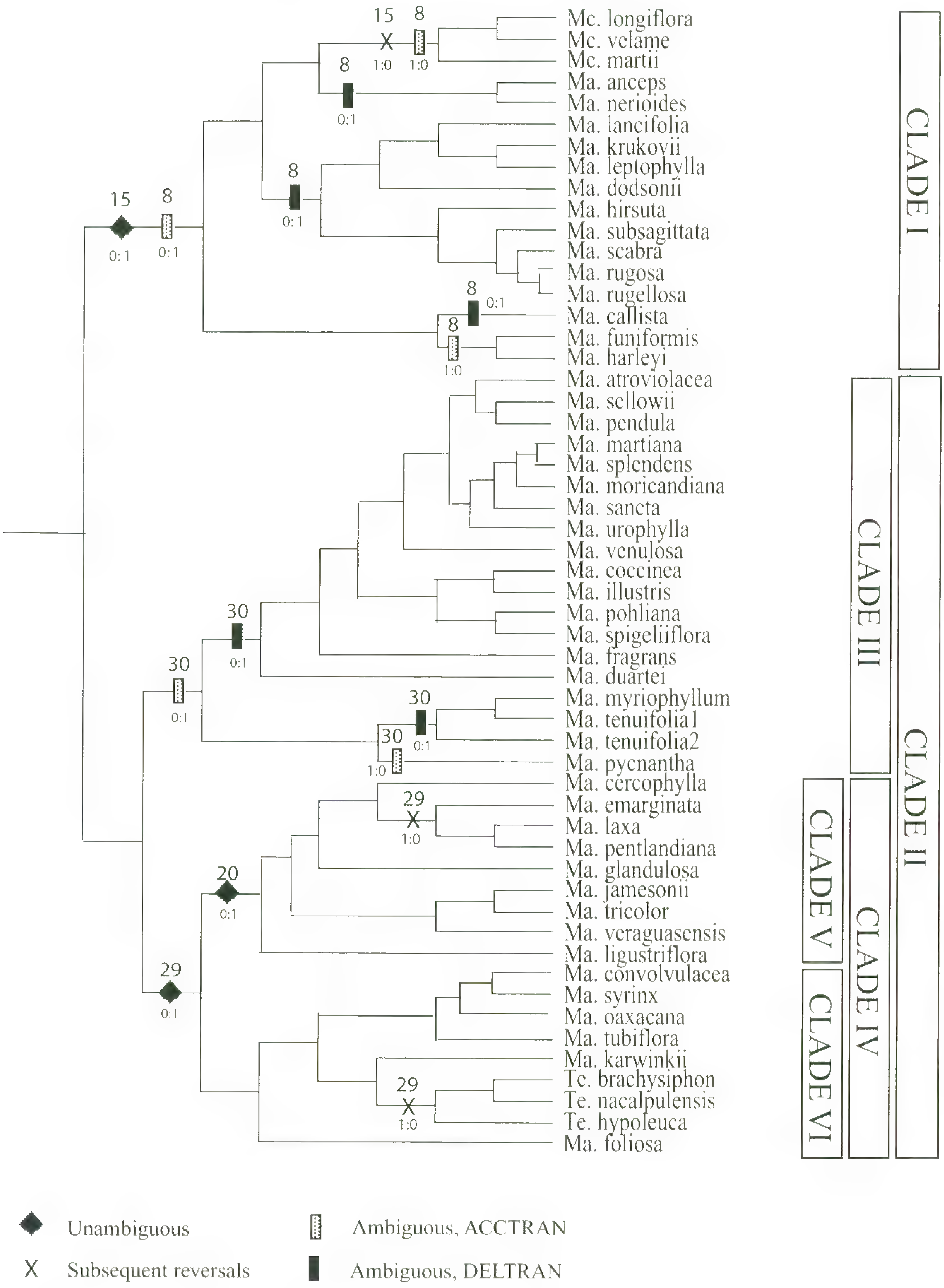

Figure 6. One of the two most parsimonious total evidence trees showing optimized morphological character-state changes within the *Mandevilla* clade. Optimizations were identical in both trees. Diamonds show unambiguously optimized character-state changes diagnostic for clades IV and V, with subsequent reversals indicated by an X. Bars denote ambiguously optimized character-state changes. Character state changes using DELTRAN optimization are indicated by solid bars; character-state changes using ACCTRAN optimization are indicated by dotted bars. All numbers above the symbols correspond to the character number as indicated in Appendix 3. The directions of character-state changes are reported below the symbols.

(Hoffmanns. ex Roem. & Schult.) K. Schum., and *M. subsagittata* (Ruiz & Pav.) Woodson), is composed of taxa that show the most common morphological pattern in the subgenus: vines with terete stems and yellow flowers, often with a red center (white flowers in *M. rugosa*), that occur mainly in forests and their bordering zones throughout the Neotropics. The second group, represented in our study by three species (*M. anceps*, *M. lancifolia*, and *M. nerioides*), is composed of taxa that have a unique set of characters within the subgenus: they are shrubs or woody lianas with strongly angled to winged stems (tetragonal in cross section) and flowers of various colors that are found mainly in the open habitats of white sand savannas and tepuis of northern South America. Neither of these two groups is monophyletic, however. All species from the first group form a strongly supported clade together with one species from the second group, *M. lancifolia*. The two remaining species of the second group, *M. anceps* and *M. nerioides*, form a strongly supported clade (BS = 100%), but this clade's relationship to the remaining species of Clade I is not resolved in our analysis. Therefore, no further conclusions on relationships and patterns of evolution within *Exothostemon* can be drawn at this time. Broader taxon sampling, especially including representatives from the poorly collected species of the winged-stem group, is needed to address these questions.

The inclusion of three species from *Mandevilla* subg. *Mandevilla* (*M. callista*, *M. funiformis*, and *M. harleyi*) in Clade I is central to understanding character evolution within the genus, because they possess characteristics of both of Woodson's (1933) subgenera. According to Woodson, *M. funiformis* has five calycine colleters in an opposite arrangement, as is characteristic for subgenus *Exothostemon*, but this species also has leaf colleters restricted to the base of the midrib, a key character of subgenus *Mandevilla*. Conversely, in *M. callista*, Woodson noted that leaf colleters are spread along the length of the midrib, as is characteristic for taxa in subgenus *Exothostemon*, while calycine colleters form a continuous ring. Woodson (1933) recognized this "intermediate" status of *M. callista* and *M. funiformis* but justified their inclusion in subgenus *Mandevilla* based on the presence of continuous calycine colleters in the former and leaf colleters restricted to the base of the midrib in the latter. We examined vouchers of the three species in order to compare morphological variation with the taxonomic descriptions provided by Woodson (1933) and Sales et al. (2006). We found that specimens of *M. funiformis* have leaf colleters restricted to the base of the midrib and calycine colleters in an opposite arrangement, confirming Woodson's observations. The same set of characters was also seen in specimens of *M. harleyi*. Our observations for *M. callista*, however, do not agree completely with Woodson's original description. We found that leaf colleters are spread along the entire midrib, but, in the specimens we studied, calycine colleters had the opposite arrangement typical for subgenus *Exothostemon*.

The well-supported inclusion of representatives of *Macrosiphonia* in Clade I is surprising and somewhat unexpected from a morphological standpoint. In *Macrosiphonia*, the leaf blade is covered by white woolly trichomes abaxially, the leaf colleters are restricted to the adaxial base of the midrib, the flowers lack a pedicel, and the calycine colleters are arranged in a continuous ring (Woodson, 1933; Ezcurra et al., 1992; Henrickson, 1996). The other species in Clade I, in contrast, have glabrous to tomentose (but never woolly) leaves with colleters spread along the midrib (except in *Mandevilla funiformis* and *M. harleyi*, where the colleters are restricted to the base), pedicellate flowers, and calycine colleters with an opposite arrangement. Increased taxon sampling and additional studies focused on features that have scarcely been addressed previously in *Mandevilla* and *Macrosiphonia* (e.g., palynology, floral ontogeny, and anatomy) could provide useful information to support relationships within this clade.

The arrangement of leaf and calycine colleters are key characters to understanding phylogenetic relationships and morphological evolution in *Mandevilla*. Colleters distributed along the entire length of the midrib were observed in species of Clade I. This character state is unique and has never been reported in any other group within Apocynaceae. Calycine colleters with opposite arrangement were also observed only in species of Clade I within the *Mandevilla* clade, but the same state has been reported in other groups of Apocynaceae, as in the Neotropical genera of tribe Echiteae (e.g., *Thenardia* HBK, *Prestonia* R. Br., and *Temnadenia* Miers)

←

Character numbers and states are as follows: 8. Leaf colleter position: 0, clustered at the base of the midrib; 1, spread along the midrib of the leaf blade. 15. Calycine colleter arrangement: 0, alternate to continuous; 1, opposite. 20. Anther base: 1, cordate; 2, truncate. 29. Proportion between the apical appendages and main body of the style head: 0, appendages shorter; 1, appendages with the same size or bigger than the main body. 30. Nectary number: 0, five; 1, two.

(Pichon, 1950; Ezcurra et al., 1992; Simões & Kinoshita, 2002). Opposite calycine colleters were unambiguously reconstructed as the ancestral state of Clade I (character no. 15, Fig. 6), but two equally parsimonious hypotheses could explain the evolution of leaf colleters in this clade (character no. 8, Fig. 6). Using ACCTRAN optimization, the presence of colleters distributed along the midrib represents a synapomorphy for Clade I, with two subsequent reversals to colleters clustered at the leaf base in both species of *Macrosiphonia* and in the *Mandevilla funiformis*/*M. harleyi* subclade. DELTRAN optimization, in contrast, suggests three parallel origins of leaf colleters distributed along the midrib: in *Mandevilla callista*, in the *M. anceps*/*M. nerioides* subclade, and in the largest subclade of Clade I. Given the unique status of this feature in Apocynaceae and its occurrence only in species of Clade I, a single origin of this state seems more likely than three parallel changes in character state, in which case it would represent another synapomorphy for Clade I. No further conclusions can be drawn from our results. Future studies focusing on the morphology and ontogeny of leaf colleters in *Mandevilla* could help to clarify the evolution of this character in the genus.

CLADE II

This clade, which comprises *Telosiphonia* and the majority of *Mandevilla* species, corresponds to Pichon's (1948) sections *Orthocaulon* and *Telosiphonia*, and for the main part to Woodson's (1933) subgenus *Mandevilla* and subgenus *Telosiphonia*. From a morphological standpoint, Clade II spans almost the entire spectrum of morphological variation found in *Mandevilla*, from subshrubs with large, showy, lilac to pink infundibuliform flowers, as in *M. sancta* (Stadelm.) Woodson, to vines with small, inconspicuous, white tubular flowers, as in *M. ligustriflora*. This clade is also represented throughout the entire geographic range of *Mandevilla*, from the southwestern United States and Mexico to subtropical Argentina.

All species from this clade share two morphological character states: leaf colleters restricted to the base of the midrib and calycine colleters with an arrangement that varies from alternate to continuous. These are, however, plesiomorphic states within the *Mandevilla* clade and therefore cannot be recognized as synapomorphies of Clade II. Simões et al. (2004) showed that colleters restricted to the leaf base is one of the four morphological synapomorphies that characterize the tribe Mesechiteae, and calycine colleters with alternate to continuous arrangement are found in the two other clades of Mesechiteae (*Mesechites* and *Forsteronia* clades), as well as in some outgroup taxa.

CLADE III

This clade is primarily composed of species of *Mandevilla* occurring in forests, savannas, and campo rupestre formations of northeastern to southern Brazil, also reaching Paraguay and Argentina. Most of these species belong to Woodson's (1933) section *Laxae*, with the exception of *M. myriophyllum* and *M. tenuifolia*, both ascribed to his section *Tenuifoliae*, and *M. pycnantha* (Steud. ex A. DC.) Woodson, attributed to section *Montanae*. With the exception of *M. pycnantha*, all species in this clade share one morphological character state: the presence of only two nectaries alternate to the carpels.

Other morphological characters, however, are more variable within this clade, in both vegetative and reproductive parts. Some species, such as *Mandevilla pendula* (Ule) Woodson and *M. urophylla* (Hook. f.) Woodson, are vines from the Atlantic Rainforest in southwestern Brazil, but others, including *M. illustris* (Vell.) Woodson, *M. pohliana* (Stadelm.) A. H. Gentry, and *M. spigeliiflora* (Stadelm.) Woodson, are small, unbranched subshrubs of savannas and campo rupestre formations from central and southern South America. Branched, woody shrubs are also common, with some species, such as *M. duartei* Markgr. and *M. venulosa* (Müll. Arg.) Woodson, endemic to specific mountain formations of southwestern Brazil. Their flowers are showy and variously colored and, in most cases, have an infundibuliform corolla. Woodson (1933) used corolla shape as a diagnostic character and defined his entire section *Laxae* according to the shared occurrence of infundibuliform corollas among its members. Even though species with an infundibuliform corolla comprise a strongly supported subclade (BS = 100%) within Clade III, this character state clearly appears to have arisen independently multiple times within *Mandevilla*, undermining its taxonomic utility.

The number of floral nectaries is an easily defined character, with no intermediate states. Most members of Clade III, with the exception of *Mandevilla pycnantha*, are characterized by the presence of two nectaries in the flower (character no. 30, Fig. 6). This state could thus be considered as a synapomorphy for Clade III, with a later reversal to five nectaries in *M. pycnantha*. However, an equally parsimonious reconstruction would involve a switch from five to two nectaries occurring independently twice: once in the clade composed by *M. myriophyllum* and *M. tenuifolia*, and again in the clade composed by the remaining species of Clade III. Given that the occurrence of two

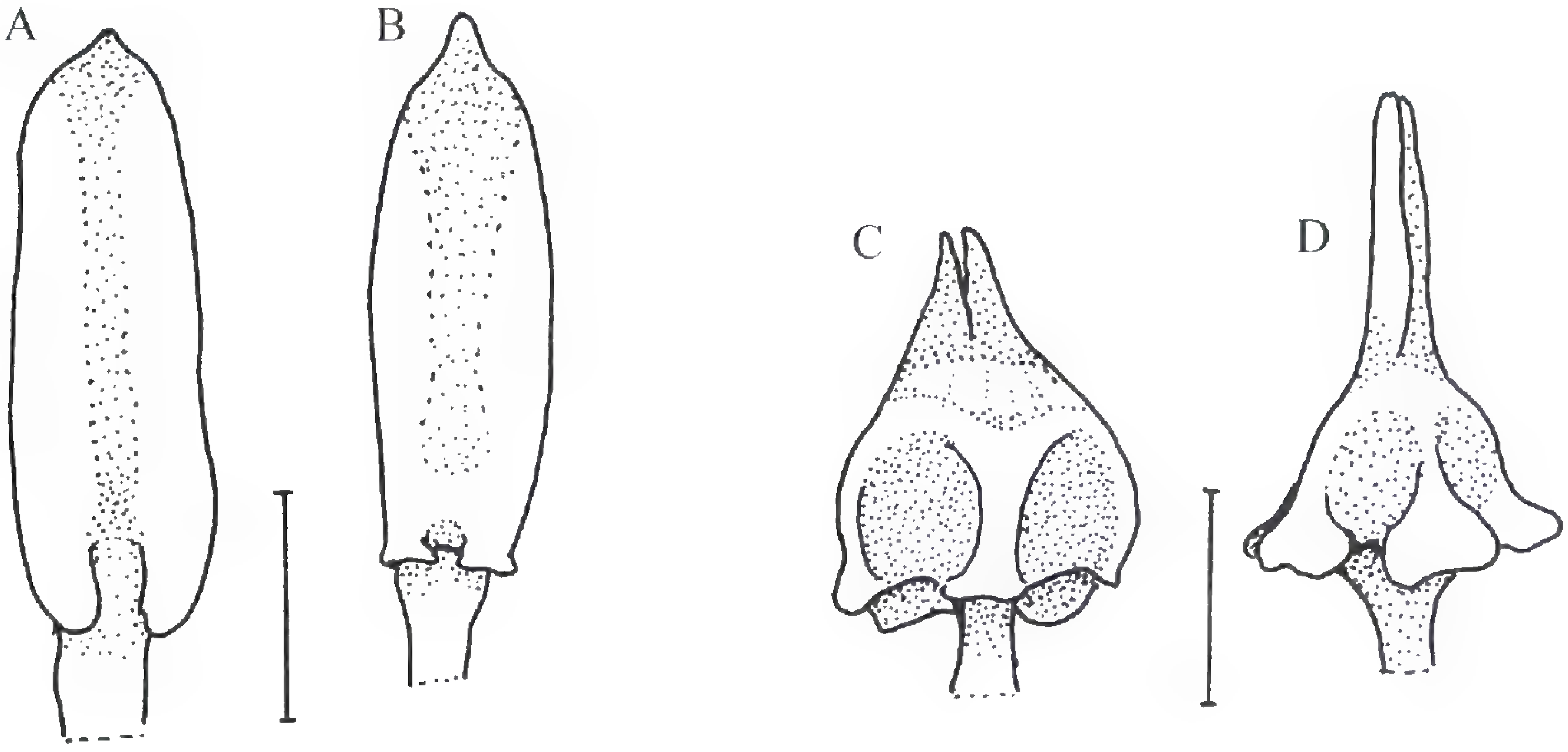

Figure 7. Diagrammatic drawings of the anther base form and style head apical appendages in *Mandevilla*. —A. *M. tenuifolia*, anther base cordate. —B. *M. veraguasensis*, anther base truncate. —C. *M. tenuifolia*, short style head appendages. —D. *M. syrinx*, long style head appendages. Scale bar = 1 mm.

nectaries is restricted to species of Clade III within *Mandevilla* and the relatively small number of taxa that exhibit this character state in Apocynaceae, the first hypothesis, of a single switch from five to two nectaries, seems more likely than two parallel changes within Clade III. Further studies focusing on the structure and development of floral nectaries in Apocynaceae, however, are needed to test these alternative hypotheses.

CLADE IV

This clade comprises a heterogeneous group of 15 species of *Mandevilla* from Woodson's (1933) sections *Laxae*, *Montaneae*, *Torosae*, and *Tubiflorae*, plus the three sampled species of *Telosiphonia*, with members distributed mainly from Mexico and the southwestern United States to northern South America, but also reaching southern Brazil and Argentina.

A morphological synapomorphy for Clade IV is the presence of elongate apical appendages of the style head that are the same size or longer than its main body (character no. 29, Fig. 6; Fig. 7). These are found in all species, with the exception of two subclades: the one formed by the three sampled species of *Telosiphonia* and the one comprising *Mandevilla emarginata* (Vell.) C. Ezcurra, *M. laxa* (Ruiz & Pav.) Woodson, and *M. pentlandiana* (A. DC.) Woodson. Two equally parsimonious reconstructions of ancestral states are possible for this character (Fig. 6). In one optimization, elongate apical appendages evolved in the ancestor of Clade IV and were independently lost in the two subclades mentioned above. In the alternative optimization, the evolution of elongate apical appendages in the ancestor of Clade V was followed by a single reversal to short appendages in the clade comprising *M. emarginata*, *M. laxa*, and *M. pentlandiana*.

CLADE V

This clade is mainly composed of species from Woodson's (1933) *Mandevilla* section *Montanae*, but three species (*M. glandulosa* (Ruiz & Pav.) Woodson, *M. laxa*, and *M. veraguasensis* (Seem.) Hemsl.) were assigned to his section *Laxae*. Most are vines, with the exception of *M. emarginata*, an unbranched subshrub, and *M. pentlandiana*, which has both vine and shrub forms. Flowers in this clade are generally salverform or tubular, white to greenish, but *M. veraguasensis*, *M. glandulosa*, and *M. laxa* have showy, infundibuliform to campanulate corollas. One morphological feature, found nowhere else in the *Mandevilla* clade, was unambiguously reconstructed as a synapomorphy of this clade: the anther base is truncate, with no discernible auricles or protruding extensions (character no. 20, Fig. 6; Fig. 7). In *M. emarginata*, *M. laxa*, and *M. pentlandiana*, auriculate anther bases can occasionally be found in some individuals, but in most cases the base is truncate. The presence of truncate anthers was used by Woodson (1933) to distinguish his section *Montanae*, although *M. pycnantha* has conspicuously auriculate anthers. Interestingly, our parsimony analyses did not support the inclusion of *M. pycnantha* in Clade V, while they firmly placed *M. glandulosa*, *M. laxa*, and *M. veraguasensis* in it. These latter species, included by Woodson (1933) in section *Laxae*, are also characterized by truncate anthers.

A distinctive aspect of Clade V is its geographical distribution. In contrast to Clade VI, which is restricted to a single region, two geographically disjunct groups can be distinguished in Clade V.

The majority of its species are found in the forests of Central America and northwestern South America. Three species (*M. emarginata*, *M. laxa*, and *M. pentlandiana*), however, occur in the Atlantic Rainforest in southern and southeastern Brazil, as well as in more arid habitats from southern Bolivia and Peru to Paraguay, Uruguay, and Argentina, with *M. emarginata* also reaching the savannas of central Brazil. The fragmentary, circum-Amazonian distribution found in this clade has also been reported in other Neotropical plant groups (e.g., Plowman, 1979, in *Brunfelsia*, Solanaceae) and might be related to the climatic fluctuations of the Quaternary, as well as the geologic history of the Andes during the Pliocene/Pleistocene.

From the Paleocene to the Miocene, the continuous occurrence of everwet climates in South America is thought to have resulted in the spread of tropical rain forests across the continent, forming a continuous belt from the Atlantic to the Pacific coast (Morley, 2000). A general cooling and/or overall reduction of precipitation on the continent during the Late Miocene and Early Pliocene resulted in the retraction of forested areas and expansion of savannas (Prance, 1982; Morley, 2000). With the simultaneous climatic fluctuations and the major uplift of the northern Andes (van der Hammen, 1974; Flenley, 1979; Morley, 2000) during the Late Tertiary and Early Quaternary and the subsequent expansion of rain forest through the Amazon basin, the northwestern part of South America became isolated from the central and southern parts of the continent. Thus the geologic and climatic history of South America during the Cenozoic could explain the close phylogenetic relationships among greatly disjunct species observed in Clade V (see Fig. 5).

CLADE VI

This clade is composed of species from Woodson's *Mandevilla* sections *Laxae* (*M. convolvulacea* (A. DC.) Hemsl., *M. oaxacana* (A. DC.) Hemsl.), *Torosae* (*M. foliosa* (Müll. Arg.) Hemsl., *M. karwinskii* (Müll. Arg.) Hemsl.), and *Tubiflorae* (*M. syrinx* Woodson, *M. tubiflora* (M. Martens & Galeotti) Woodson), plus genus *Telosiphonia*, all of which occur in deserts and dry forests of Mexico and the southwestern United States. Morphological traits in this clade are extremely variable, especially those related to flower structure. *Mandevilla syrinx* and *M. tubiflora* have many-flowered inflorescences bearing small, tubular, white flowers, whereas *M. convolvulacea* and *M. oaxacana* have few-flowered inflorescences with showy, yellow, infundibuliform flowers. The most striking floral morphology of this clade is found in *Telosiphonia*, characterized by long, narrowly tubular, white flowers forming 1- to few-flowered inflorescences.

Although species of Woodson's (1933) sections *Torosae* and *Tubiflorae* are restricted to this clade, they do not form monophyletic groups, and thus their continued recognition might be questionable. The distinction between these two sections is based on nectary height: in section *Torosae*, the nectaries are shorter than the ovary, whereas in section *Tubiflorae* they are the same size or taller than the ovary. We observed that species of section *Torosae* always have nectaries taller than the ovary, but the same condition occurs in three other species from this clade, all of which belong to different sections sensu Woodson (1933): *Mandevilla foliosa* (sect. *Torosae*), and *M. convolvulacea* and *M. oaxacana* (both in sect. *Laxae*). Nectaries shorter than the ovary are found in all *Telosiphonia* species and in *M. karwinskii*, which together form a strongly supported subclade (BS = 100%).

The sister relationship between *Mandevilla karwinskii* and species of *Telosiphonia*, which has never been proposed before, is congruent with their geographic distribution and habitat preferences. Both taxa are rhizomatous shrubs occurring sympatrically in the deserts of Mexico and the southwestern United States. Apart from their short nectaries, morphological traits are quite different between *M. karwinskii* and species of *Telosiphonia*, especially leaf indument, flower size, and style head structure.

The striking similarity in morphology between species of *Telosiphonia* and *Macrosiphonia* is the most extreme example of parallel evolution in the *Mandevilla* clade. The two genera, each of which comprises a well-supported subclade nested within the *Mandevilla* clade (*Macrosiphonia* in Clade I and *Telosiphonia* in Clade VI, see Fig. 5), occur in disjunct geographic areas that roughly coincide with the extreme northern and southern range of *Mandevilla*. *Macrosiphonia* is found in the savannas of southern South America in arid, usually sandy cerrado and campo rupestre vegetation from southern Bolivia and Peru to central Brazil, Paraguay, Uruguay, and Argentina, whereas *Telosiphonia* is restricted to the arid zones of Mexico and the southwestern United States. Despite their geographic disjunction, the two genera share a suite of morphological characteristics. Both are erect shrubs or subshrubs, sometimes rhizomatous, with a well-developed underground storage system and leaves covered by a dense, wooly indument on the abaxial surface. The most remarkable similarities, however, are related to flower structure. In both genera, flowers are white and tubular, with some of the longest corolla tubes in Apocynaceae, reaching up to 17 cm in *Macrosiphonia longiflora*,

and are only fully open at dusk, when they produce a distinctive scent, suggesting pollination by hawkmoths.

The apparent parallelism in vegetative characters observed in these two groups could be explained as an adaptation to similar environmental conditions. A shrubby, erect habit, the presence of a dense indument covering both vegetative and reproductive organs, and well-developed underground storage organs such as tubers and xylopods are common traits of plants of open, seasonally dry habitats (Rizzini, 1997; Dallman, 1998). On the other hand, parallelism in floral structure is more likely driven by pollinator preferences. The distinctive features shared by *Macrosiphonia* and *Telosiphonia* are typical of the sphingophilous (hawkmoth) pollination syndrome reported by many authors (e.g., Vogel, 1954; Faegri & van der Pijl, 1966; Baker & Hurd, 1968; Endress, 1994; Galetto, 1997). Reports of hawkmoths visiting flowers of various *Telosiphonia* and *Macrosiphonia* species are congruent with the hypothesis of hawkmoth pollination. For example, two hawkmoth species, *Manduca sexta* L. and *Hyles lineata* Fabricius, have been observed visiting *Telosiphonia nacapulensis* Felger & Henr. and *T. brachysiphon* (Torr.) Henr. in the Sonoran Desert of southern Arizona (R. Raguso, pers. comm., 2004). In Cordoba Province and in the El Palmar National Park, Entre Ríos Province, Argentina, *Manduca sexta*, *M. rustica* Fabricius, and *Agrius cingulata* Fabricius have been found carrying pollen of *Macrosiphonia petraea* (A. St.-Hil.) K. Schum attached only to the very tips of their proboscis (A. Cocucci, pers. comm., 2004). Given the remarkable length of the floral tube of this plant (ca. 105 mm), it is reasonable to expect that only insects with a very long proboscis could reach the nectar (Marcela Moré, in prep.).

Conclusions

The phylogenetic results presented here show that *Mandevilla*, as circumscribed by Pichon (1948), is monophyletic, but Woodson's (1933) circumscription of the genus is paraphyletic. *Quiotania*, *Macrosiphonia*, and *Telosiphonia* are nested within *Mandevilla* and therefore should be included in its synonymy. Representatives from *Macrosiphonia* and *Telosiphonia* form distinct clades embedded within *Mandevilla*, and their striking morphological similarities may have evolved in parallel, possibly as a result of similar selective pressures driven by colonization of open, dry habitats and hawkmoth pollination.

All infrageneric taxa within *Mandevilla* proposed by both Woodson (1933) and Pichon (1948) were found to be paraphyletic or polyphyletic, with the exception of Woodson's section *Tenuifoliae* and Pichon's sections *Megasiphon* and *Telosiphonia*. Recognition of these three sections is, however, untenable for the moment, as this would require recognizing additional sections that lack clear morphological synapomorphies. Six major clades were recognized within *Mandevilla* in our study, although only three have unambiguous morphological synapomorphies. It is hoped that more detailed morphological studies in *Mandevilla* could uncover additional characters that might prove useful for delimitation within this group. Until such evidence becomes available, we think it is most prudent to withhold from erecting a new intrageneric classification of *Mandevilla*.

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Appendix 1. Voucher information and Genbank accession numbers for the taxa used in this paper. Additional vouchers selected for morphological analyses are indicated by an asterisk (*).

Species	Voucher/citation	*rpl*16 Intron	*rps*16 Intron	*trn*S^{GCU}-*trn*G^{UUC} Intergenic spacer	*trn*K Intron	*mat*K Gene
Allomarkgrafia brenesiana Woodson	Costa Rica, *Endress 97-06* (Z)	AY597546	AY597580	AY597614	DQ522660	DQ522591
Allomarkgrafia plumeriiflora Woodson	Costa Rica, *Morales 9338* (INB)	DQ522730	DQ522812	DQ522771	DQ522661	DQ522592
Beaumontia grandiflora Wall.	Cultivated, Bot. Gard. Munich, *G. Gerlach 5/06* (M); *India, Feb. 1909, *coll. Native collector s.n.* (Z)	AY597547	AY597581	AY597615	DQ522662	Z98174
Chonemorpha fragrans (Moon) Alston	Cultivated, Queensland, Australia, *Forster 2009* (BRI); * India, *Ridsale 109* (Z)	AY597548	AY597582	AY597616	DQ522663	DQ522593
Forsteronia acouci (Aubl.) A. DC.	French Guiana, *Prévost 3720* (CAY); * Peru, *Revilla 291* (Z); * Venezuela, *Breteler 5029* (Z)	AY597549	AY597583	AY597617	DQ522664	DQ522594
Forsteronia refracta Müll. Arg.	Brazil, *Yamamoto 02/108* (UEC)	DQ522731	DQ522813	DQ522772	DQ522665	DQ522595
Forsteronia velloziana (A. DC.) Woodson	Brazil, *Simões 343* (UEC)	AY597550	AY597584	AY597618	DQ522666	DQ522596
Macrosiphonia longiflora (Desf.) Müll. Arg.	Brazil, *Schütz Rodrigues 1227* (UEC); * Brazil, *Simões 47, 859, 930* (UEC)	AY597551	AY597585	AY597619	DQ522667	DQ522597
Macrosiphonia martii Müll. Arg.	Brazil, *Simões 1245* (UEC); * Brazil, *Duarte 2445* (RB); * Brazil, *Simões 1205, 1206* (UEC)	AY597552	AY597586	AY597620	DQ522668	DQ522598
Macrosiphonia velame (A. St.-Hil.) Müll. Arg.	Brazil, *Simões 1199* (UEC); * Brazil, *Leitão-Filho 15307* (UEC); * Brazil, *Kinoshita 2000/67* (UEC)	DQ522732	DQ522814	DQ522773	DQ522669	DQ522599
Mandevilla anceps Woodson	Venezuela, *Huber & Medina 5793* (Z)	DQ522733	DQ522815	DQ522774	DQ522670	DQ522600
Mandevilla atroviolacea (Stadelm.) Woodson	Brazil, *Meireles 1290* (UEC)	DQ522734	DQ522816	DQ522775	DQ522671	DQ522601
Mandevilla callista Woodson	Ecuador, *Webster & Castro 31319* (Z); * Ecuador, *Céros 2874* (AAU); * Ecuador, *Gentry 12457, 30842* (Z)	DQ522735	DQ522817	DQ522776	DQ522672	DQ522602
Mandevilla cercophylla Woodson	Ecuador, *Matezki 420* (Z)	DQ522736	DQ522818	DQ522777	DQ522673	DQ522603
Mandevilla coccinea (Hook. & Arn.) Woodson	Brazil, *Flores 452* (UEC)	DQ522737	DQ522819	DQ522778	DQ522674	DQ522604
Mandevilla convolvulacea (A. DC.) Hemsl.	Mexico, *Alvarado 162* (MEXU)	DQ522738	DQ522820	DQ522779	DQ522675	DQ522605
Mandevilla dodsonii A. H. Gentry	Ecuador, *Fallen 875* (Z)	DQ522739	DQ522821	DQ522780	DQ522676	DQ522606
Mandevilla duartei Markgr.	Brazil, *Simões 1281* (UEC)	DQ522740	DQ522822	DQ522781	DQ522677	DQ522607

Appendix 1. Continued.

Species	Voucher/citation	*rpl*16 Intron	*rps*16 Intron	*trn*S^{GCU}-*trn*G^{UUC} Intergenic spacer	*trn*K Intron	*mat*K Gene
Mandevilla emarginata (Vell.) C. Ezcurra	Brazil, *Quast 1* (UEC); * Brazil, *Bicudo 1235* (UEC); * Brazil, *Oliveira 35* (SP)	DQ522741	DQ522823	DQ522782	DQ522678	DQ522608
Mandevilla foliosa (Müll. Arg.) Hemsl.	Mexico, *Reína 2000-447* (Z)	DQ522742	DQ522824	DQ522783	DQ522679	DQ522609
Mandevilla fragrans (Stadelm.) Woodson	Brazil, *Pansarin & Mickeliunas 1022* (UEC)	DQ522743	DQ522825	DQ522784	DQ522680	DQ522610
Mandevilla funiformis (Vell.) K. Schum.	Brazil, *Simões 1105* (UEC); * Brazil, *Custódio-Filho 733* (SP); * Brazil, *Leitão-Filho 10764* (UEC); * Brazil, *Shepherd & Vidal 11221* (UEC)	DQ522744	DQ522826	DQ522785	DQ522681	DQ522611
Mandevilla glandulosa (Ruiz & Pav.) Woodson	Ecuador, *Matezki 127* (Z)	DQ522745	DQ522827	DQ522786	DQ522682	DQ522612
Mandevilla harleyi M. F. Sales, Kin-Gouv. & A. O. Simões	Brazil, *Simões 1303* (UEC); * Brazil, *Harley 25194* (SPF)	AY597559	AY597593	AY597627	DQ522683	DQ522613
Mandevilla hirsuta (Rich.) K. Schum.	Brazil, *Kinoshita 02/114* (UEC)	DQ522746	DQ522828	DQ522787	DQ522684	DQ522614
Mandevilla illustris (Vell.) Woodson	Brazil, *Kinoshita & Matsumoto 0000/562* (UEC)	DQ522747	DQ522829	DQ522788	DQ522685	DQ522615
Mandevilla jamesonii Woodson	Ecuador, *Jorgensen 1467* (Z)	DQ522748	DQ522830	DQ522789	DQ522686	DQ522616
Mandevilla karwinskii (Müll. Arg.) Hemsl.	Mexíco, *Fishbein 2966* (ARIZ)	AY597553	AY596587	AY597621	DQ522687	DQ522617
Mandevilla krukovii Woodson	Brazil, *Kirkbride & Lleras 2907* (Z)	DQ522749	DQ522831	DQ522790		
Mandevilla lancifolia Woodson	Venezuela, *Davidse & Huber 14887* (Z)	DQ522750	DQ522832	DQ522791		
Mandevilla laxa (Ruiz & Pav.) Woodson	Argentina, *Galetto 809* (CORD); * Argentina, *Hatschbach 40681* (Z); * Argentina, *Novara 8347, 8568* (Z)	DQ522751	DQ522833	DQ522792	DQ522688	DQ522618
Mandevilla leptophylla (A. DC.) K. Schum.	Venezuela, *Steyermark 119835* (Z)	DQ522752	DQ522834	DQ522793	DQ522689	DQ522619
Mandevilla ligustriflora Woodson	Ecuador, *Matezki 340* (Z); * Ecuador, *Espinosa 1547* (MO)	AY597554	AY596588	AY597622	DQ522690	DQ522620
Mandevilla martiana (Stadelm.) Woodson	Brazil, *Simões & Pansarin 1100* (UEC)	DQ522753	DQ522835	DQ522794	DQ522691	DQ522621
Mandevilla moricandiana (A. DC.) Woodson	Brazil, *Simões 1130* (UEC)	DQ522754	DQ522836	DQ522795	DQ522692	DQ522622
Mandevilla myriophyllum (Taub.) Woodson	Brazil, *Pansarin 878* (UEC)	AY597555	AY596589	AY597623	DQ522693	DQ522623
Mandevilla nerioides Woodson	Colombia, *Franco 618* (Z)	DQ522755	DQ522837	DQ522796		
Mandevilla oaxacana (A. DC.) Hemsl.	Mexico, *Alvarado 190* (MEXU)	DQ522756	DQ522838	DQ522797	DQ522694	DQ522624

Appendix 1. Continued.

Species	Voucher/citation	*rpl*16 Intron	*rps*16 Intron	*trn*S^{GCU}-*trn*G^{UUC} Intergenic spacer	*trn*K Intron	*mat*K Gene
Mandevilla pendula (Ule) Woodson	Brazil, *Ribeiro 2520* (UEC)	DQ522757	DQ522839	DQ522798	DQ522695	DQ522625
Mandevilla pentlandiana (A. DC.) Woodson	Brazil, *Simões 1272* (UEC); * Brazil, *Silva 1081* (UEC); * Brazil, *Lewinsohn 15901* (UEC)	DQ522758	DQ522840	DQ522799	DQ522696	DQ522626
Mandevilla pohliana (Stadelm.) A. H. Gentry	Brazil, *Feres 98/49* (UEC)	DQ722759	DQ522841	DQ522800	DQ522697	DQ522627
Mandevilla pycnantha (Steud. ex A. DC.) Woodson	Brazil, *Yamamoto 02/107* (UEC)	AY597556	AY596580	AY597625	DQ522698	DQ522628
Mandevilla rugellosa (Rich.) L. Allorge	French Guiana, *Prévost 3720* (CAY); * Surinam, *Lindeman 1976* (Z)	AY597561	AY597595	AY597629	DQ522699	DQ522629
Mandevilla rugosa (Benth.) Woodson	Brazil, *Simões 1204* (UEC)	AY597557	AY597591	AY597625	DQ522700	DQ522630
Mandevilla sancta (Stadelm.) Woodson	Brazil, *Simões 1060* (UEC)	DQ522760	DQ522842	DQ522801	DQ522701	DQ522631
Mandevilla scabra (Hoffmanns. ex Roem. & Schult.) K. Schum.	Brazil, *Simões 1126* (UEC)	AY597558	AY597592	AY597626	DQ522702	DQ522632
Mandevilla sellowii (Müll. Arg.) Woodson	Brazil, *Ribeiro 2522* (UEC)	DQ522761	DQ522843	DQ522802	DQ522703	DQ522633
Mandevilla spigeliiflora (Stadelm.) Woodson	Brazil, *Gomes 513* (UEC)	DQ522762	DQ522844	DQ522803	DQ522704	DQ522634
Mandevilla splendens (Hook. f.) Woodson	Brazil, *Simões 1268* (UEC)	AY597560	AY597594	AY597628	DQ522705	DQ522635
Mandevilla subsagittata (Ruiz & Pav.) Woodson	Mexico, *Alvarado 288* (MEXU)	DQ522763	DQ522845	DQ522804	DQ522706	DQ522636
Mandevilla syrinx Woodson	Mexico, *Calzada 21305* (MEXU)	DQ522764	DQ522846	DQ522805	DQ522707	DQ522637
Mandevilla tenuifolia (J. C. Mikan) Woodson, acc. 1	Brazil, *Simões 1171* (UEC)	AY597562	AY597596	AY597630	DQ522708	DQ522638
Mandevilla tenuifolia (J. C. Mikan) Woodson, acc. 2	Brazil, *Kinoshita & Matsumoto 00/609* (UEC)	AY597563	AY597597	AY597631	DQ522709	DQ522639
Mandevilla tricolor Woodson	Ecuador, *Jorgensen 1484* (Z)	DQ522765	DQ522847	DQ522806		
Mandevilla tubiflora (M. Martens & Galeotti) Woodson	Mexico, *Alvarado 106* (MEXU)	DQ522766	DQ522848	DQ522807	DQ522710	DQ522640
Mandevilla urophylla (Hook. f.) Woodson	Brazil, *M. P. Quast 6* (UEC)	DQ522767	DQ522849	DQ522808	DQ522711	DQ522641
Mandevilla venulosa (Müll. Arg.) Woodson	Brazil, *Simões 1107* (UEC)	AY597564	AY597598	AY597632	DQ522712	DQ522642
Mandevilla veraguasensis (Seem.) Hemsl.	Costa Rica, *Endress 97-76* (Z)	AY597565	AY597599	AY597633	DQ522713	DQ522643
Mesechites mansoanus (A. DC.) Woodson	Brazil, *Simões 1087* (UEC)	AY597567	AY597601	AY597635	DQ522714	DQ522644
Mesechites minimus (Britton & P. Wilson) Woodson	Cuba, Feb. 2001, *Nilsson s.n.* (Z)	AY597568	AY597602	AY597636	DQ522715	DQ522645

Appendix 1. Continued.

Species	Voucher/citation	*rpl*16 Intron	*rps*16 Intron	*trn*S^{GCU}-*trn*G^{UUC} Intergenic spacer	*trn*K Intron	*mat*K Gene
Mesechites roseus (A. DC.) Miers	Cuba, Feb. 2001, *Nilsson s.n.* (Z)	AY597569	AY597603	AY597637	DQ522716	DQ522646
Mesechites trifidus (Jacq.) Müll. Arg.	Ecuador, *Liede & Meve 3471* (UBT)	DQ522768	DQ522850	DQ522809	DQ522717	DQ522647
Odontadenia lutea (Vell.) Markgr.	Brazil, *Kinoshita 2002/56* (UEC)	AY597570	AY597604	AY597638	DQ522718	DQ522648
Pachypodium geayi Costantin & Bois	Cultivated, Bot. Gard. Chèvreloup, *Lieberherr s.n.* (unvouchered)	AY597571	AY597605	AY597640	DQ522719	DQ522649
Pachypodium lamerei Drake	Cultivated, Zürich Bot. Gart., *Simões 1333* (Z)	AY597572	AY597606	AY597639	DQ522720	DQ522650
Prestonia riedelii (Müll. Arg.) Markgr.	Brazil, *Simões 1274* (UEC)	AY597573	AY597607	AY597641	DQ522721	DQ522651
Rhodocalyx rotundifolius Müll. Arg.	Brazil, *Kinoshita 2000/66* (UEC)	AY597574	AY597608	AY597642	DQ522722	DQ522652
Secondatia densiflora A. DC.	Brazil, *Simões 1218* (UEC)	AY597575	AY597609	AY597643	DQ522723	DQ522653
Telosiphonia brachysiphon (Torr.) Henr.	U.S.A., *Jenkins 00-185* (TUC); * U.S.A., *Worthington 25068* (TEX)	AY597576	AY597610	AY597644	DQ522724	DQ522654
Telosiphonia hypoleuca (Benth.) Henr.	Mexico, *Reina 2000-362* (Z); * Mexico, *Richardson 1526* (TEX)	AY597579	AY597611	AY597645	DQ522725	DQ522655
Telosiphonia nacalpulensis Felger & Henr.	U.S.A., Arizona, July 2000, *Van Devender s.n.* (Z)	DQ522769	DQ522851	DQ522810	DQ522726	DQ522656
Tintinnabularia gratissima J. F. Morales	Mexico, *Ventura 107* (ENCB)	DQ522770	DQ522852	DQ522811	DQ522727	DQ522657
Tintinnabularia mortonii Woodson	Mexico, *Breedlove 34900* (TEX)	AY597578	AY597612	AY597646	DQ522728	DQ522658
Trachelospermum jasminoides (Lindl.) Lem.	Cultivated, Zürich Bot. Gard., *Simões 1334* (Z)	AY597577	AY597613	AY597647	DQ522729	DQ522659

Appendix 2. Morphological matrix. ? signifies missing data. Polymorphic states are indicated by numbers in brackets. Characters and coding for character states as in Appendix 3.

Taxon	Character states for characters 1–32
Allomarkgrafia brenesiana	10000111000001000001101032100010
Allomarkgrafia plumeriiflora	10000111000001000001101032100010
Beaumontia grandiflora	10010100000101000000102021000001
Chonemorpha fragrans	10020100000001000000101021000000
Forsteronia acouci	1000011101000103001110 11{23}2200001
Forsteronia refracta	100001110100010300111011{23}2200001
Forsteronia velloziana	100001110000010300111010{23}2200001
Macrosiphonia longiflora	20000111101011010001101032200000
Macrosiphonia martii	20000111101011010001101032200000
Macrosiphonia velame	20000111101011010001101032200000
Mandevilla anceps	20100112001001100001101132200000
Mandevilla atroviolacea	10000111001001000001101032200100
Mandevilla callista	10000112001101100101101132200000
Mandevilla cercophylla	10000111011001010002101032201000
Mandevilla coccinea	20000111001001010001101032200100
Mandevilla convolvulacea	10000111001001000001101032201011
Mandevilla dodsonii	10000112001101100101101132200000
Mandevilla duartei	20000111001001000001101032200100
Mandevilla emarginata	200001110011010200 0{12}101032200000
Mandevilla foliosa	20000111001001010001101032201010
Mandevilla fragrans	10000111001001000001101032200100
Mandevilla funiformis	10000111001001100101101132200000
Mandevilla glandulosa	10000111001001000002101032201000
Mandevilla harleyi	20000111001001100101101132200000
Mandevilla hirsuta	10000111001101100101101132200000
Mandevilla illustris	20020111001001000001101032200100
Mandevilla jamesonii	10000111001001010002101032201000
Mandevilla karwinskii	20000111001001010001101032201000
Mandevilla krukovii	10000112001101100101101132200000
Mandevilla lancifolia	{12}0100{12}12001001100001101032200000
Mandevilla laxa	1002111100100100000{12}101032200000
Mandevilla leptophylla	10021112001001100101101132200000
Mandevilla ligustriflora	10000111011001000002101032201000
Mandevilla martiana	{12}0021111001001000001101032200100
Mandevilla moricandiana	10021111001001000001101032200100
Mandevilla myriophyllum	20020111001001010001101032200100
Mandevilla nerioides	20100112001001100001101?32200000
Mandevilla oaxacana	10000111001001000001101032201011
Mandevilla pendula	10000111001001000001101032200100
Mandevilla pentlandiana	{12}00001110011010200 0{12}101032200000
Mandevilla pohliana	20020111001001000001101032200100
Mandevilla pycnantha	20000111001001010001101032200000
Mandevilla rugellosa	10000112001101110101101132200000
Mandevilla rugosa	10000112001001100101101132200000
Mandevilla sancia	{12}0021111001001000001101032200100
Mandevilla scabra	10000112001001100101101132200000
Mandevilla sellowii	10021111001001000001101032200100
Mandevilla spigeliiflora	20000111001001000001101032200100
Mandevilla splendens	10021111001001000001101132200101
Mandevilla subsagittata	10020112001001110101101?32200000
Mandevilla syrinx	10000111001001020001101032201011
Mandevilla tenuifolia 1	20020111001001010001101032200100
Mandevilla tenuifolia 2	20020111001001010001101032200100
Mandevilla tricolor	10000111001001010002101032201000
Mandevilla tubiflora	10000111001001020001101032201010

Appendix 2. Continued.

Taxon	Character states for characters 1–32
Mandevilla urophylla	10021111001001000001101032200100
Mandevilla venulosa	20000111001001000001101032200100
Mandevilla veraguasensis	10000111001001000002102032201000
Mesechites mansoanus	10000111000001010001101032100010
Mesechites minimus	1000011100?001010001101032100010
Mesechites roseus	1000011100?001010001101032100010
Mesechites trifidus	10000111000001010001101032100010
Odontadenia lutea	10020100000001000000111021000000
Pachipodium geayi	000-0000000000-00010000-00000000
Pachipodium lamerei	000-0000000000-00000000-00000000
Prestonia riedelii	11010100001101111000111010010000
Rhodocalyx rotundifolius	21000100000101111000101010010010
Secondatia densiflora	10020100000001010000111021000000
Telosiphonia brachysiphon	20000111101001010001101032200000
Telosiphonia hypoleuca	20000111101001010001101032200000
Telosiphonia nacalpulensis	20000111101001010001101032200000
Tintinnabularia gratissima	1000011101?001000001101032100010
Tintinnabularia mortonii	1000011101?101000001102032100010
Trachelospermum jasminoides	10020100000001010000101021000000

Appendix 3. Characters and character states for the morphological matrix used in the cladistic analyses.

1. **Habit**: 0, trees; 1, lianas or vines; 2, erect shrubs or subshrubs, these often with a xylopod.
2. **Latex**: 0, white; 1, translucent.
3. **Stem in cross section**: 0, circular; 1, pentagonal.
4. **Nodal colleters**: 0, interpetiolar; 1, intrapetiolar; 2, continuous. Colleters are small glandular structures found on the margin or in axillary position to both vegetative and reproductive organs in the Apocynaceae (Thomas, 1991). Their number and organization have been traditionally used as taxonomic characters in the family. The arrangement of colleters on the branch nodes constitutes an easily coded character that has not received taxonomic scrutiny in *Mandevilla* and related genera.
5. **Spiny ring of nodal colleters**: 0, absent; 1, present. In some species of *Mandevilla*, the nodal colleters are greatly expanded and form a somewhat spiny crown around the nodes.
6. **Phyllotaxis**: 0, alternate; 1, opposite.
7. **Leaf colleters**: 0, absent; 1, present.
8. **Leaf colleter position**: 0, clustered at the base of the leaf blade adaxially; 1, spread along the midrib of the leaf blade adaxially.
9. **Abaxial leaf surface**: 0, thick indument of white wooly trichomes absent; 1, thick indument of white wooly trichomes present.
10. **Domatia**: 0, absent; 1, present.
11. **Inflorescence type**: 0, branched (cymose); 1, unbranched (racemose).
12. **Bracts**: 0, scarious; 1, petaloid.
13. **Pedicel**: 0, present; 1, absent.
14. **Calycine colleters**: 0, absent; 1, present.
15. **Calycine colleter arrangement**: 0, alternate to continuous; 1, opposite.
16. **Corolla shape**: 0, infundibuliform or campanulate to tubular-campanulate; 1, salverform; 2, tubular; 3, rotate.
17. **Annular corona**: 0, absent; 1, present.
18. **Form of the lower corolla tube**: 0, straight; 1, curved.
19. **Stamens**: 0, completely included; 1, tips of the anthers exserted, stamens ± completely exserted.
20. **Anther base**: 0, strongly sagittate; 1, cordate; 2, truncate.
21. **Anther guide-rails**: 0, composed mainly of endothecial thickenings; 1, composed mainly of sclerenchyma.
22. **Dorsal side of anthers**: 0, completely glabrous; 1, with trichomes.
23. **Filament length**: 0, anthers ± sessile; 1, < 1 cm long; 2, > 3 cm long.
24. **Junction of filament and anther connection**: 0, flat; 1, with a globose swelling.
25. **Anther/style head union**: 0, anthers attached by a circular patch of trichome-like cells; 1, anthers attached by a horseshoe-shaped rim of hairs; 2, anthers attached by a horseshoe-shaped rim of hairs and a narrow longitudinal strip; 3, anthers attached by cellular fusion.
26. **Style head shape in cross section**: 0, circular or subcircular; 1, pentagonal; 2, with five strongly projecting ribs.
27. **Style head ribs**: 0, absent; 1, restricted to the base; 2, along the entire length of the body of the style head.
28. **Collar or wreath at base of style head**: 0, absent; 1, present.
29. **Proportion between the apical appendages and main body of the style head**: 0, < 1:1; 1, 1:1 or appendages bigger than the main body. The style head is divided in two portions: two apical appendages and a massive main body. The appendages are variable in size within different species of *Mandevilla*, and their size in proportion to the main body constitutes a character that has never been used before in the genus.
30. **Nectaries number**: 0, five; 1, two.
31. **Nectaries height**: 0, smaller than the ovary; 1, equal or greater than the ovary.
32. **Ovary indument**: 0, absent; 1, present.

REVISIÓN DE LAS ESPECIES DE *AXONOPUS* (POACEAE, PANICOIDEAE, PANICEAE), SERIE *SUFFULTI*[1,2]

Ana María Cialdella, Osvaldo Morrone y Fernando O. Zuloaga[3]

RESUMEN

El presente trabajo comprende la revisión taxonómica de las especies del género *Axonopus* P. Beauv. serie *Suffulti* G. A. Black. Esta serie se caracteriza por incluir especies perennes, frecuentes en sabanas y campos, sobre suelo arcilloso o arenoso, con afloramientos rocosos, hasta los 3500 m. Las plantas son rizomatosas o estoloníferas, con vainas conduplicadas y láminas desde angostamente lineares a linear-lanceoladas, planas o plegadas totalmente o bien solo en la base. Las inflorescencias son exertas, ubicadas en el ápice de las cañas, compuestas por racimos espiciformes, en número variable, mayormente digitados. El raquis de los racimos es triquetro, sinuoso, con ángulos hispídulos, a veces con pelos largos y rígidos. La lemma superior y la pálea superior ambas endurecidas, son castaño oscuro, de superficie papilosa y lustrosa. Dentro de la serie *Suffulti* se consideran 16 especies, mayormente distribuidas en Sudamérica, con *A. ciliatifolius* Swallen y *A. jeanyae* Davidse endémicas de Belice y Panamá respectivamente. Se incluyen descripciones de los caracteres morfológicos y de los microcaracteres del antecio superior, una clave para la identificación de las especies, y para cada una de ellas se proporciona una descripción, sinonimia, distribución geográfica e ilustraciones de los caracteres con valor taxonómico. Finalmente, se lectotipifica la serie *Suffulti* y *A. ramboi* G. A. Black es incluida en la sinonimia de *A. argentinus* Parodi.

ABSTRACT

The taxonomic revision of species of the genus *Axonopus* P. Beauv. series *Suffulti* G. A. Black is presented. This series includes perennial species, frequently growing in savannas and in grasslands, on argillaceous or sandy ground with rocky outcrops, at altitudes up to 3500 m. The plants are rhizomatous or stoloniferous, with conduplicate sheaths and narrowly linear to linear-lanceolate blades, flat to folded along their entire length, or open toward the apex. The inflorescences are exserted from the apex of the culms; they consist of spiciform racemes of variable number, mainly digitate. The rachis of each raceme is triquetrous, sinuous, with hispidulous angles, sometimes with long and rigid hairs. The upper lemma and the upper palea are indurate, dark brown, papillose, and shiny. Sixteen species are here considered within *Axonopus* series *Suffulti*, principally distributed in South America, with *A. ciliatifolius* Swallen and *A. jeanyae* Davidse endemic species of Belize and Panama, respectively. Description of morphological characters and microcharacters of the upper floret, a key to identify the species, descriptions, synonymy, geographical distribution, and illustrations of characters of taxonomic value are given. Finally, lectotypification of series *Suffulti* is established, and *A. ramboi* G. A. Black is included in *A. argentinus* Parodi as a synonym.

Key words: *Axonopus* series *Suffulti*, Centroamérica, Poaceae, Sudamérica.

Axonopus P. Beauv. es un género americano distribuído desde el sur de Estados Unidos de América hasta el norte y centro de Argentina y Uruguay. Comprende alrededor de 110 especies (Black, 1963; Clayton & Renvoize, 1986), mayormente concentradas en la región tropical, siendo Brasil, Venezuela y Colombia los países con mayor riqueza en especies (Giraldo-Cañas, 2000b; Zuloaga et al., 2006). Este género habita frecuentemente por debajo de los 1000 m, constituyendo un importante elemento de las sabanas naturales. Desde el punto de vista económico, algunas de sus especies tienen importancia como es el caso de *A. compressus* (Sw.) P. Beauv., "carpet-grass", utilizada para césped; asimismo, ésta, junto con otras especies—*A. fissifolius* (Raddi) Kuhlm., *A. scoparius* (Flüggé) Kulhm., *A.*

[1] Deseamos agradecer a Vladimiro Dudás y Francisco Rojas (Instituto Darwinion) la elaboración de las ilustraciones, a Alejandra Garbini (Instituto Darwinion) la composición de las fotografías, y a Alejandro Escobar (Instituto Darwinion), Myrian Esther Giordano y Alejandro Reynoso (CITEFA), su colaboración en las observaciones realizadas con el microscopio electrónico de barrido. Agradecemos también a los directores y curadores de los herbarios consultados la gentileza en el préstamo de material, al Board of Trustees of Royal Botanic Gardens, Kew por el envío de imágenes de ejemplares tipo depositados en ese herbario y a todo el personal del Instituto Darwinion por brindarnos siempre su ayuda. Parte de este estudio se llevó a cabo con fondos de la National Geographic Society (subsidio #6825-00) y de la Myndel Botanica Foundation, que permitieron realizar trabajos de campo, del Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PIP-02131) y de la Agencia Nacional de Promoción Científica y Tecnológica (ANPCYT, PICT-11739).

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purpusii (Mez) Chase, *A. suffultus* (Mikan ex Trin.) Parodi—son forrajeras naturales (Nicora & Rúgolo de Agrasar, 1987; Giraldo-Cañas, 2000a; Anton, 1982).

El trabajo más integral sobre *Axonopus*, del cual derivaron los estudios florísticos posteriores, fue realizado por G. A. Black (1963), quien reconoció 109 especies y 20 variedades dentro del género. Black agrupó las especies en secciones y series, siguiendo básicamente la clasificación anteriormente propuesta por Chase (1911). La desaparición de Black en 1957, tuvo como consecuencia que el manuscrito fuera finalmente ordenado por L. B. Smith, lo que justifica que el manejo del trabajo resulte complejo y que los límites entre los taxones sean poco claros. Por otra parte, *Axonopus* no cuenta con un volumen importante de colecciones en los herbarios, y, de hecho, algunas entidades sólo se encuentran representadas por el material tipo. Recientemente, el interés por trabajos florísticos en Centroamérica y América del Sur ha llevado a incrementar considerablemente las colecciones del género. Por esta razón, se considera oportuno intensificar el estudio en este género, y lograr así una clasificación más natural.

El objetivo del presente trabajo es contribuir al conocimiento de las especies de *Axonopus* incluidas en la serie *Suffulti* G. A. Black de la sección *Axonopus*. Para la identificación de las especies estudiadas, se utilizaron principalmente caracteres exomorfológicos vegetativos, tales como el hábito y el tamaño, forma y disposición de las hojas, así como también caracteres relacionados con la inflorescencia, entre ellos el indumento del raquis, el número de racimos, el tamaño de las espiguillas y la nerviación de la gluma superior y la lemma inferior. Se proporciona una clave para la identificación de las especies incluidas en la serie, descripción, sinonimia, distribución geográfica y observaciones de cada una de ellas e ilustraciones de los caracteres de valor taxonómico.

Materiales y Métodos

Para la identificación de las especies, se han seguido los métodos clásicos de la taxonomía. Se examinó el material depositado en los herbarios: BAA, K, LPB, MEXU, MO, NY, SI, US, USZ, VEN (Holmgren et al., 1990). Una lista de las especies tratadas en la serie *Suffulti* de *Axonopus* se incluyen en el Apéndice 1. Dentro del material examinado de cada especie sólo se citaron ejemplares representativos de cada país; una lista completa de los especímenes estudiados, ordenados alfabéticamente por coleccionista, se encuentran al final del texto (Apéndice 2).

Se realizaron observaciones de la lemma y pálea del antecio superior, en vista topográfica mediante microscopia electrónica de barrido, en un equipo Zeiss DSM 940 A, que funciona en el Instituto de Botánica Darwinion. Previamente al metalizado, se procedió a la remoción parcial de las ceras epicuticulares, mediante ultrasonido, con el material sumergido en xileno durante 60 minutos (Dávila & Clark, 1990). Luego el material se dejó secar a temperatura ambiente, para su posterior metalizado con oro-paladio. La película utilizada para fotografiar esta superficie fue AGFAPAN APX 100 Professional 120. Por otra parte, se analizaron otras muestras en un ESEM Philips Electroscan 2010, Microscopio Electrónico de Barrido Ambiental (environmental scanning electron microscope), que funciona en el Edificio de Materiales, del Instituto de Investigaciones Científicas y Técnicas de las Fuerzas Armadas (CITEFA). En este caso, las muestras fueron observadas sin preparación previa (no necesitan metalizado ni punto crítico) y en condiciones de humedad relativa por encima del 50%, a un presión de entre 3 y 5 Torr y una temperatura no mayor de 5°C. Para crear estas condiciones el ESEM cuenta con una cámara para muestras, con presión ajustable que va desde 0.1 a 20 Torr y una platina por efecto Peltier que va en ± 50 grados centígrados a partir de la temperatura ambiente.

Historia del Género

El género *Axonopus* fue establecido por Palisot de Beauvois (1812), sobre la base de cuatro especies originalmente pertenecientes al género *Milium* L.—*M. compressum* Sw., *M. digitatum* Sw., *M. cimicinum* L. y *M. paniceum* Sw.—y una quinta especie, *Axonopus aureus* P. Beauv. Beauvois señala que *Axonopus* se halla estrechamente relacionado con *Milium* y *Paspalum* L., y lo distingue por las inflorescencias digitadas.

Chase (1911) afirma que el carácter que identifica este género es la presencia de espiguillas solitarias, además de la forma de su inflorescencia. Diversos autores en trabajos posteriores siguieron el criterio de reconocer *Axonopus* como género, tales como Roemer y Schultes (1817), Hooker (1896), Hitchcock (1908), Kuhlmann (1922), Henrard (1922), Parodi (1938), Pilger (1940), Swallen (1948), Black (1950) y Dedecca (1956). Otros autores, en cambio, consideraron *Axonopus* como grupo o sección dentro del género *Paspalum*, entre los que pueden citarse Trinius (1826, 1828–1836), Nees (1829), Hackel (1887), Bentham (1881), Bentham y Hooker (1883), Doell (1877) y Mez (1917, 1921). Cabe señalar que fue Nees (1829) quien por primera vez notó la posición reversa de las

espiguillas en *Axonopus*, carácter también observado por Hackel (1887) y utilizado por Hitchcock (1908, 1909) y Chase (1911) para delimitar al género.

Chase (1911), por otra parte, fue el primer autor que propuso la subdivisión de *Axonopus* en tres secciones: *Lappagopsis* (Steud.) Chase, *Cabrera* (Lag.) Chase y *Axonopus*. Este criterio fue adoptado por Pilger (1940) y por Black (1963). Según este último autor, la sección *Axonopus*, en la cual incluye 96 especies, se distingue por presentar raquis glabro, escabroso o piloso, rara vez con pelos papilosos blancos, espiguillas glabras o pilosas pero no papiloso-pilosas y antecios pajizos a castaño oscuro. La sección *Lappagopsis*, compuesta por tres especies, se caracteriza por sus inflorescencias con raquis y espiguillas cubiertos con pelos papilosos tiesos blanquecinos y antecios castaño oscuro. Finalmente, la sección *Cabrera*, con 10 especies, agrupa entidades con raquis densamente piloso, los pelos rígidos, papilosos, dorados, frecuentemente fasciculados en la base de las espiguillas, espiguillas glabras o esparcidamente pilosas y antecios castaño oscuro. Giraldo-Cañas (2000b) establece la sección *Senescentia* sobre la base de *A. senescens* (Döll) Henrard, y la distingue de las secciones *Cabrera* y *Lappagopsis* por tener antecio superior pajizo y pelos del raquis blanquecinos a hialinos.

En la sección *Axonopus*, Black (1963) propuso cinco series: Axonopus, Barbigeri, Suffulti, Capillares y Fastigiati, que se distinguen por el indumento del raquis, el color del antecio superior, el número de racimos, la nerviación de gluma superior y lemma inferior, la forma de las hojas y el hábito de la planta. Al describir estas series, Black (1963) no designó la especie tipo para cada una de ellas, siendo entonces nombres inválidos de acuerdo al *Código Internacional de Nomenclatura Botánica* (art. 10.2; Greuter et al., 2000).

Dentro de la serie Suffulti, Black (1963) incluyó 19 especies. Estas se identifican por su hábito perenne, sus inflorescencias con raquis hispídulo generalmente con escasos pelos blanquecinos no papilosos, dispersos o concentrados en la base de los pedicelos, rara vez con raquis glabro, sus espiguillas provistas de gluma superior y lemma inferior con nerviación poco notable y generalmente sin nervio central, glabras o con pelos esparcidos, cortos, no papilosos y por sus antecios oscuros y lustrosos aún cuando inmaduros.

Caracteres Morfológicos de las Especies de la Serie *Suffulti*

Hábito

Las especies de esta serie son perennes, rizomatosas, rara vez estoloníferas, gráciles o bien robustas. Generalmente, están provistas de un rizoma corto y grueso, de nudos muy próximos, carácter que genera plantas densamente cespitosas. Un caso interesante es el de *Axonopus pressus* (Nees ex Steud.) Parodi, con innovaciones cubiertas por vainas pajizas, notablemente dísticas, ascendentes u horizontales, tempranamente subterráneas, luego aéreas. En *A. argentinus* Parodi, el rizoma es estoloniforme, es decir subterráneo pero delgado, con entrenudos largos, dando lugar a una planta laxamente cespitosa. En *A. cuatrecasasii* G. A. Black, y excepcionalmente en *A. suffultus*, se observa en cambio un típico estolón, arraigado en los nudos y a partir del cual se originan vástagos distantes entre sí.

Las cañas son herbáceas o subleñosas, cilíndricas o levemente comprimidas, a veces con un surco longitudinal, simples o ramificadas en la base o en la zona media, paucinodes o plurinodes, con entrenudos mayormente glabros y nudos conspicuos, glabros a vilosos.

Caracteres foliares

Las vainas son abiertas, lateralmente comprimidas, carinadas o redondeadas en el dorso, glabras a hirsutas o densamente vilosas. En algunas especies (*Axonopus flabelliformis* Swallen, *A. suffultus*, *A. magallanesiae* Giraldo-Cañas) la disposición de las vainas en la base de la planta es conspicuamente dística, equitante, carácter que genera plantas lateralmente comprimidas de aspecto iridáceo. En *A. suffultus* además las vainas son glaucas, con tintes violáceos. La zona del cuello es de aspecto variable: puede ser inconspicuo, o bien notable por su color más intenso que la vaina o por la presencia de pelos, a veces concentrados hacia los bordes de la vaina. *Axonopus succulentus* G. A. Black se distingue del resto de las especies por la presencia de aurículas.

La lígula es membranácea, corta, glabra o pubescente, y su borde es siempre densamente pestañoso. En las especies estudiadas no se encontraron diferencias significativas de valor taxonómico.

Las láminas son conduplicadas, desde angostamente lineares hasta linear-lanceoladas, planas o plegadas totalmente o bien solo en la base, con ápice agudo a obtuso, a veces retuso en *Axonopus elegantulus* (J. Presl) Hitchc., *A. magallanesiae*, *A. pressus*, *A. succulentus* y ocasionalmente bi-partido en *A. pressus*. La consistencia varía desde herbácea (*A. pennellii* G. A. Black, *A. polydactylus* (Steud.) Dedecca) hasta rígida. El indumento de las láminas es marcadamente variable, hallándose ejemplares con láminas glabras a densamente vilosas.

INFLORESCENCIAS

Las inflorescencias son exertas, ubicadas en el ápice de las cañas, compuestas por racimos espiciformes, mayormente digitados, siendo los basales alternos. El número de racimos es variable en esta serie, siendo poco numerosos (2–6(–10)) en *Axonopus arcuatus* (Mez) G. A. Black, *A. elegantulus*, *A. cuatrecasasii*, *A. gracilis* G. A. Black, *A. hoehnei* G. A. Black, *A. magallanesiae*, *A. ciliatifolius* Swallen, *A. jeanyae* Davidse y *A. ramosus* Swallen; en cambio, en *A. suffultus*, *A. polydactylus*, *A. pennellii*, *A. succulentus* y *A. pressus*, el número de racimos es mayor (de 11–34, excepcionalmente menos). En *A. argentinus* y *A. flabelliformis* Swallen el número de racimos varía entre cinco y 20. Este caracter es de utilidad para el reconocimiento de las especies, solo asociado a otros caracteres.

El raquis de los racimos es triquetro, sinuoso, con cara dorsal plana y provista en general de un nervio central conspicuo, la cara ventral con una costilla central prominente. Generalmente los ángulos del raquis son hispídulos y pueden presentar pelos largos y rígidos a la altura de la base de los pedicelos, ocasionalmente dispersos sobre los ángulos. Este carácter ha sido tradicionalmente empleado con valor diagnóstico a nivel específico.

ESPIGUILLA

Las espiguillas se disponen solitarias, unilateralmente en dos hileras sobre el raquis, generalmente alternas, rara vez geminadas. Son múticas, la gluma inferior se encuentra ausente y la gluma superior se ubica externa con respecto al raquis. La flor inferior está reducida a la lemma inferior de aspecto glumiforme y ubicada hacia el raquis. Tanto la gluma superior como la lemma inferior son membranáceas, generalmente 2–3-nervias, más rara vez 4–5-nervias, siendo sus nervios poco conspicuos. Ambas son generalmente de igual longitud que el antecio, ocasionalmente mayores o bien la gluma superior puede ser menor, dejando ver el ápice de la lemma fértil. En cuanto al indumento, pueden ser glabras o con pelos dispersos, a veces concentrados a ambos lados de los nervios.

ANTECIO SUPERIOR

Textura

La forma del antecio superior es sumamente constante, de contorno oblongo, dorsiventralmente comprimido, con ápice agudo u obtuso, compuesto por la lemma superior y la pálea superior ambas endurecidas, glabras, a veces con escasos pelitos cortos en el ápice de la lemma, castaño oscuro, de superficie papilosa y lustrosa (Fig. 1A). Los márgenes de la lemma se encuentran abrazando a la pálea, cubriendo los 2/3 de la superficie, encerrando el ápice de la pálea. La lemma y la pálea se hallan compuestas de células largas rectangulares, más de dos veces más largas que anchas, con las paredes anticlinales longitudinales y tranversales onduladas (Fig. 1B).

Ornamentación

La epidermis abaxial de la lemma y de la pálea presentan papilas simples, cuerpos de sílice, macropelos o micropelos. Las papilas son simples, una por célula, excéntricas, próximas a la pared transversal distal, distribuidas regularmente en hileras longitudinales (Figs. 1C, D, F, 2A, C, E, F). Las papilas poseen el ápice uniformemente redondeado, excepcionalmente éstas pueden terminar en una punta aguda, muy pequeña, como se observó en algunas superficies de lemma y pálea de *Axonopus polydactylus*, *A. ramosus* y *A. suffultus* (Fig. 2E). Los cuerpos de sílice son halteriformes, de eje corto, o cruciformes, equidimensionales, exfoliados, presentes en la zona apical de la lemma y de la pálea, como por ejemplo en *A. arcuatus*, *A. argentinus*, *A. flabelliformis*, *A. hoehnei*, *A. magallanesiae*, *A. pennellii*, *A. polydactylus*, *A. ramosus*, *A. succulentus* y *A. suffultus* (Figs. 1B, 2B, D). La presencia de macropelos es variable, pueden estar presentes o ausentes, cuando presentes son unicelulares, escasos, simples, de paredes engrosadas y paralelas, y se localizan en la región apical de la lemma, en *A. argentinus*, *A. jeanyae*, *A. magallanesiae*, *A. pennellii*, *A. ramosus*, *A. polydactylus* y *A. suffultus* (Fig. 1A, E, F); ocasionalmente, se observaron macropelos aislados en la base de la pálea en *A. flabelliformis*, *A. pennellii* y *A. suffultus* (Fig. 2F). Los micropelos pueden estar presentes o ausentes, cuando presentes éstos son bicelulares, fusiformes, del tipo “panicoide”, con la célula distal dos a tres veces más larga que la célula basal, de ápice subagudo y se observaron en el ápice de la lemma y de la pálea de *A. arcuatus*, *A. hoehnei*, *A. pennellii*, *A. polydactylus*, *A. ramosus* y *A. succulentus*.

DISTRIBUCIÓN GEOGRÁFICA

Las especies de *Suffulti* se distribuyen desde Belice hasta Uruguay y la provincia de Buenos Aires en Argentina. En Centro América crecen dos especies, *Axonopus ciliatifolius* y *A. jeanyae*, la primera endémica de Belice y la segunda endémica de Panamá. El mayor número de especies se concentran en Sudamérica con una distribución restringida. En el Escudo Guayanés habitan *A. gracilis*, *A. ramosus*, *A.*

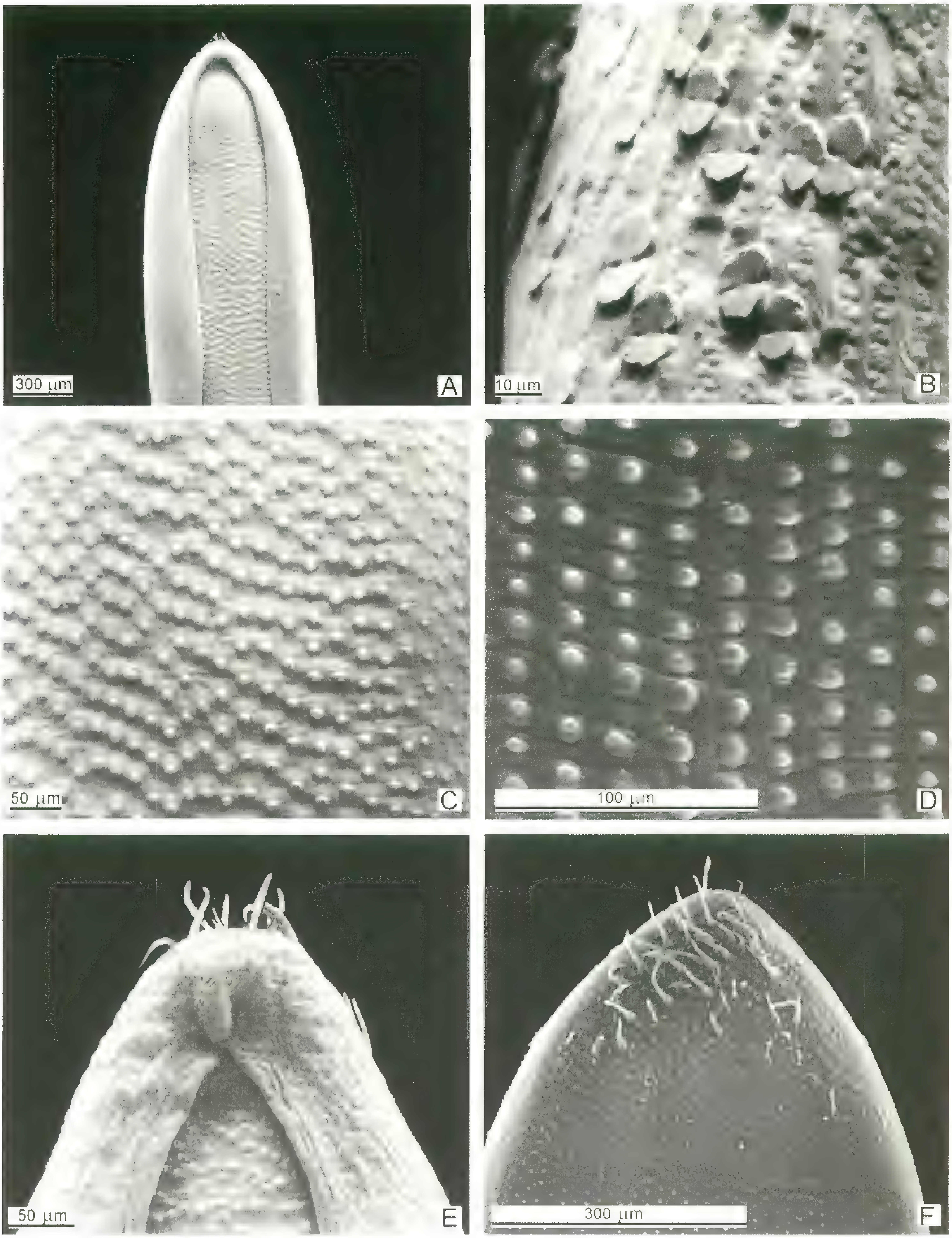

Figura 1. Fotomicrografías de antecios superiores de *Axonopus* P. Beauv. A–C. *A. argentinus* Parodi (de *Burkart 25270*). —A. Vista general de un antecio, del lado de la pálea. —B. Detalle de cuerpos de sílice en el borde de la lemma. —C. Detalle de la superficie de la lemma con papilas. —D. *A. flabelliformis* Swallen (del holotipo *Hitchcock 17275*). Detalle de la superficie de la lemma con papilas. —E. *A. jeanyae* Davidse (del holotipo *Davidse & C. W. Hamilton 23570*). Detalle del ápice del antecio visto del lado de la pálea, con macropelos y cuerpos de sílice en la lemma. —F. *A. pennellii* G. A. Black (del holotipo *Pennell 1539*). Detalle del ápice del antecio visto del lado de la lemma, con macropelos, micropelos y papilas.

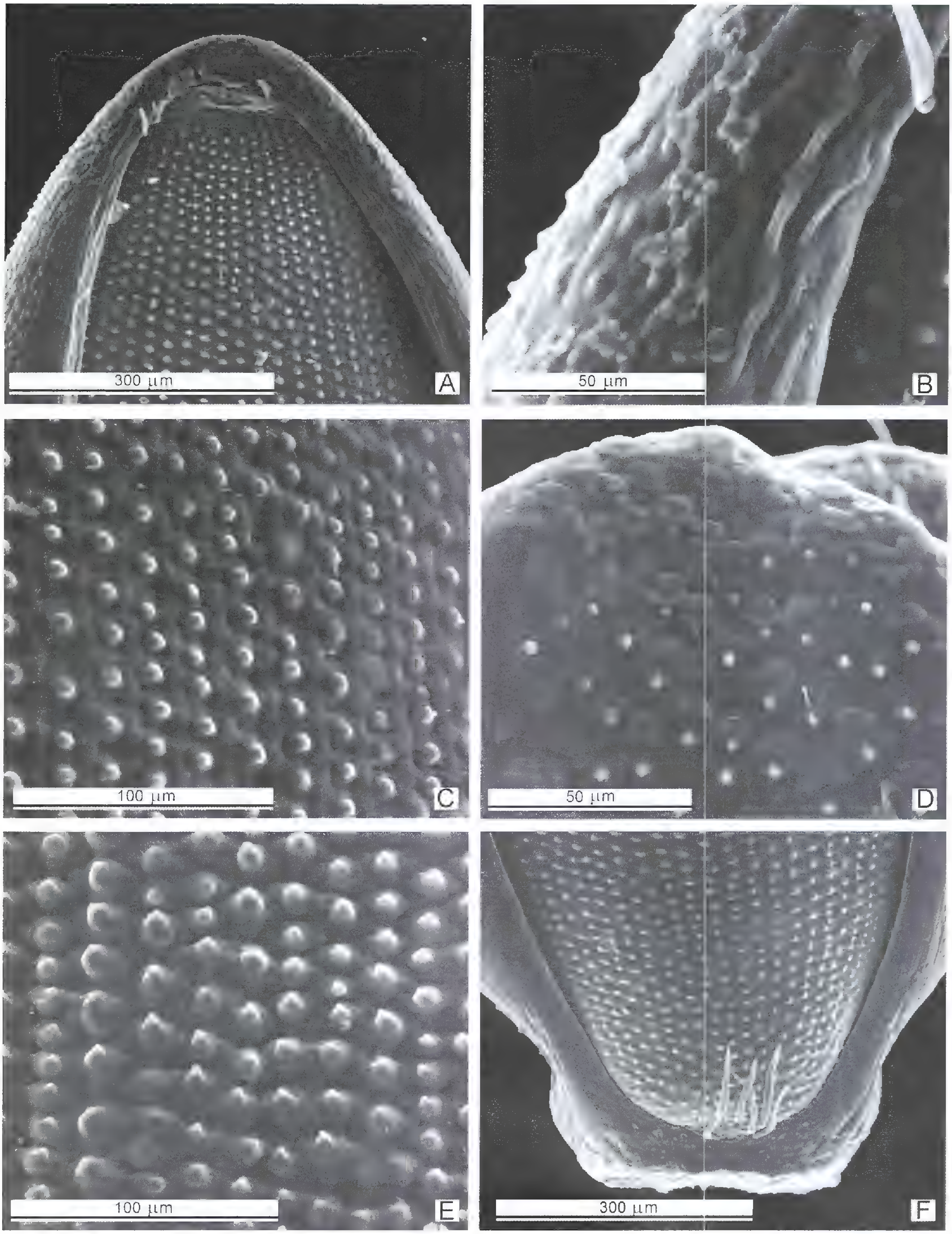

Figura 2. Fotomicrografías de antecios superiores de *Axonopus* P. Beauv. A–C. *A. magallanesiae* Giraldo-Cañas (del holotipo *Huber 12995*). —A. Detalle del ápice del antecio visto del lado de la pálea. —B. Detalle de cuerpos de sílice en el borde de la lemma. —C. Detalle de papilas de la lemma. D–E. *A. polydactylus* (Steud.) Dedecca (del isotipo *Salzmann s.n.*, US 2855750). —D. Detalle de cuerpos de sílice y papilas en el ápice de la lemma. —E. Detalle de papilas de la lemma. —F. *A. suffultus* (Mikan ex Trin.) Parodi (del isotipo *Mikan s.n.*, US 80029). Detalle de la base del antecio visto del lado de la pálea con macropelos y papilas.

Tabla 1. Características morfológicas de las series (sensu Black, 1963) de la sección *Axonopus*.

	Series				
Caracteres	Axonopus	Barbigeri	Capillares	Fastigiati	*Suffulti*
Ciclo de vida	perenne	perenne	anual	perenne	perenne
Antecio superior	pajizo	pajizo	pajizo a castaño claro	pajizo	castaño oscuro
Gluma superior	glabra o pilosa	glabra o pubescente	glabra o pubescente	largamente ciliada	glabra o pilosa
Nervios de la gluma superior y lemma inferior	notorios	prominentes	notorios	notorios	notorios a tenues
Nervio medio	generalmente ausente	presente	generalmente ausente	presente	ausente
Raquis	glabro	glabro	glabro	papiloso-piloso	glabro a piloso

pennellii y *A. magallanesiae*. *Axonopus flabelliformis* y *A. cuatrecasasii* presentan una distribución disyunta, con especies en el Escudo de las Guayanas y también en el centro de Bolivia. *Axonopus elegantulus* es endémica de Perú y crece en altitudes medias de los Andes. *Axonopus succulentus* es una especie endémica de la región oriental del Paraguay. *Axonopus arcuatus*, *A. polydactylus* y *A. hoehnei* se encuentran restringidas al centro y este de Brasil. *Axonopus pressus* es la especie que posee más amplia distribución creciendo desde el noreste de Brasil hasta la región oriental de Paraguay y noreste de Bolivia. *Axonopus argentinus* y *A. suffultus* se encuentran restrigidas al sur de Brasil, este de Paraguay, Uruguay y noreste de Argentina.

Discusión

Las especies de la serie *Suffulti* son fácilmente distinguibles de otros miembros del género *Axonopus* por la presencia del antecio superior castaño oscuro y lustroso. De acuerdo con los caracteres morfológicos estudiados sus especies se caracterizan por tener inflorescencias exertas y axilares, con racimos mayormente digitados, raquis de los racimos glabro o piloso, cuando piloso con pelos rígidos usualmente próximos a la base de los pedicelos, la lemma y la pálea del antecio superior son endurecidas, castaño oscuro y de superficie papilosa lustrosa.

Dentro del género *Axonopus* las especies de la serie *Suffulti* comparten con las especies incluidas en la secciones *Cabrera* y *Lappagopsis* la presencia de antecio superior castaño oscuro. La sección *Lappagopsis* incluye tres especies, *A. brasiliensis* (Spreng.) Kuhlm., *A. chaseae* G. A. Black y *A. herzogii* (Hack.) Hitchc. (Black, 1963; Giraldo-Cañas, 2002). Esta sección posee una distribución restringida en América del Sur, en Bolivia, Brasil y Paraguay, y crece en áreas abiertas de serranías y cerros, sabanas de arenas blancas, en cerrados y en afloramientos rocosos del Escudo Brasileño. Sus especies se caracterizan por presentar el raquis y/o las espiguillas densamente pilosas, con pelos blanquecinos, rígidos, de base tuberculada. La sección *Cabrera*, de amplia distribución en América desde el sur de México e islas del Caribe hasta Bolivia y centro y sudeste de Brasil, incluye dos especies, *A. aureus* y *A. chrysoblepharis* (Lag.) Chase (Giraldo-Cañas, 2001). Esta sección se caracteriza por tener el raquis densamente papiloso-piloso, con pelos dorados, frecuentemente fasciculados y asociados a la base de la inserción de la espiguilla.

Black (1963) incluye la serie *Suffulti* dentro de la sección *Axonopus* y caracteriza a las especies pertenecientes a esta sección por tener el raquis glabro, escabroso o escasamente piloso, los pelos de base no tuberculada, espiguillas glabras a laxamente pilosas. Esta sección es la más compleja del género e incluye ca. 60 especies de amplia distribución en América, alguna de sus especies habita en el Paleotrópico. En la Tabla 1 se presentan las diferencias entre las series de *Axonopus* sect. *Axonopus*.

Tratamiento Taxonómico

Axonopus P. Beauv., Ess. Agrostogr. 12: 154. 1812. TIPO: *Axonopus aureus* P. Beauv. (lectotipo, designado por Hitchcock, Contr. U.S. Natl. Herb. 12: 142. 1908).

Plantas mayormente perennes, rara vez anuales, cespitosas, rizomatosas o estoloníferas; cañas herbáceas o subleñosas; vainas comprimidas lateralmente, carinadas o redondeadas en el dorso, abiertas; lígula membranácea breve, con borde generalmente ciliado, a veces pestañoso; aurículas mayormente ausentes, excepcionalmente presentes; láminas lineares a linear-lanceoladas, conduplicadas, raro convolutas, plegadas

hasta el ápice o solo en la base, herbáceas a rígidas, frecuentemente concentradas en la base de la planta, a veces dispuestas a lo largo de las cañas, o bien en la porción mediana de las mismas. Cañas floríferas exertas, con inflorescencias solitarias, terminales o bien terminales y axilares, naciendo del último nudo caulinar, compuestas por varios a numerosos racimos espiciformes, unilaterales, simples, digitados o subdigitados, más rara vez ubicados a lo largo de un eje, paniculados; raquis de los racimos triquetro, cara dorsal plana, cara ventral con costilla central, escabroso o piloso, frecuentemente sinuoso; espiguillas unifloras, solitarias, unilaterales, alternas en 2 hileras a lo largo de la cara ventral del raquis a cada lado de la costilla central. Espiguillas elipsoides, de contorno oblongo, dorsalmente comprimidas, múticas, orientadas con el dorso de la lemma inferior hacia el raquis y la gluma superior hacia afuera del raquis, cortamente pediceladas, pedicelos escabriúsculos o con algunos pelos largos; gluma inferior ausente; gluma superior y lemma inferior membranáceas, subiguales, tan largas como el antecio, a veces ligeramente mayores, o bien gluma superior más corta que el antecio, 2–5-nervias, de superficie papilosa, opacas o lustrosas; lemma superior y pálea superior endurecidas, subiguales, castañas, la lemma con márgenes levemente involutos abrazando los bordes de la pálea; lodículas 2; estambres 3; estilos 2. Fruto una cariopsis; embrión 1/3–1/2 de la longitud de la cariopsis; hilo elíptico o cortamente linear. Número básico de cromosomas $x = 10$ (Hickenbick et al., 1975; Morrone et al., 1995). Estructura anatómica C_4 (Kranz del subtipo MS) (Brown, 1977).

Género con aproximadamente 100 especies, de América cálida, desde Estados Unidos de América hasta la Argentina y Uruguay.

Observaciones. Chase (1911), eligió *Axonopus compressus* como especie tipo del género, ignorando deliberadamente la decisión de Hitchcock (1908), probablemente porque *A. aureus* es una especie muy pobremente descrita, basada en un ejemplar tipo del cual se desconoce su procedencia y no ha sido localizado (Anton, 1982). Por esta razón, Black (1963), siguiendo el concepto de Chase, consideró *A. aureus* como taxón dudoso y lo excluyó del género.

Axonopus serie **Suffulti** G. A. Black, Frontiers Pl. Sci. 5: 127. 1963. TIPO: *Paspalum suffultum* Mikan ex Trin., 1821 [= *Axonopus suffultus* (Mikan ex Trin.) Parodi] (lectotipo, aquí designado).

Plantas perennes gráciles o robustas, rizomatosas o estoloníferas; vainas lateralmente comprimidas; láminas conduplicadas, lineares a linear-lanceoladas, planas o plegadas. Inflorescencias con pocos a numerosos racimos (2 a más de 30); raquis de los racimos y pedicelos frecuentemente pilosos. Gluma superior y lemma inferior con nervios inconspicuos, el nervio medio usualmente ausente; antecio superior castaño oscuro, finamente papiloso, lustroso.

Black (1963) al describir la serie *Suffulti* no designó especie tipo. En el presente tratamiento se seleccionó como lectotipo a *Paspalum suffultum* por ajustarse al protólogo de la serie.

Clave para Distinguir las Especies de *Axonopus* Serie *Suffulti*

1. Vainas basales conspicuamente dísticas, equitantes; plantas lateralmente comprimidas, de aspecto iridáceo, densamente cespitosas 2
1′. Vainas basales dispuestas alrededor de la caña, no dísticas; plantas no lateralmente comprimidas 4
2(1). Gluma superior y lemma inferior 4–5-nervias; inflorescencias compuestas por 3–5 racimos de 4–8 cm de largo, láminas de (3–)6–9(–10) cm de largo; plantas de 30–50 cm de altura; espiguillas de 2.1–2.3(–2.5) mm de largo . . . . *A. magallanesiae*
2′. Gluma superior y lemma inferior 2(–3)-nervias; inflorescencias formadas por 12–23(–40) racimos de 5–22 cm de largo; plantas de 55–150 cm de altura; espiguillas de (1.3–)1.6–2.5 mm de largo 3
3(2). Plantas con vainas generalmente glaucas con zonas violáceas, rara vez pajizas; láminas predominantemente basales; gluma superior 1.9–2.5 mm de largo, igual o levemente mayor que el antecio; sur de Brasil, Uruguay, Paraguay y noreste y centro de la Argentina . . . . *A. suffultus*
3′. Plantas con vainas pajizas, glabras; láminas dispuestas a lo largo de las cañas; gluma superior 1.2–1.5(–2.2) mm de largo, generalmente menor que el antecio; Bolivia, norte de Brasil, Guyana, Guayana Francesa, Surinam, Venezuela . . . . *A. flabelliformis*
4(1). Vainas con aurículas; plantas robustas con cañas simples, de 5 mm de diámetro . . *A. succulentus*
4′. Vainas sin aurículas; plantas gráciles o robustas, con cañas simples o ramificadas, generalmente menores de 5 mm diámetro 5
5(4). Plantas estoloníferas, gráciles, levemente cespitosas . . . . *A. cuatrecasasii*
5′. Plantas con rizomas cortos y gruesos, o bien con rizomas estoloniformes, todos subterráneos . . 6
6(5). Cañas profúsamente ramificadas en la porción media, con las hojas mayormente dispuestas en la porción apical de las cañas, o bien en las ramificaciones laterales . . . . *A. ramosus*
6′. Cañas simples o laxamente ramificadas en los nudos basales, con las hojas distribuidas mayormente en la región basal de la planta . . . 7
7(6). Plantas con rizomas estoloniformes, falciformes o bien rectos, con entrenudos largos . . *A. argentinus*
7′. Plantas con rizomas cortos, gruesos a delgados, con entrenudos cortos 8

8(7). Plantas con innovaciones gruesas, curvas, ascendentes, originalmente subterráneas, ligeramente comprimidas y cubiertas por numerosos catáfilos rígidos, pajizos, notablemente dísticos; láminas rígidas, de ápice subagudo frecuentemente hendido cuando viejas . . . . *A. pressus*

8′. Plantas con innovaciones aéreas, macolladas; láminas generalmente herbáceas, de ápice agudo a obtuso, no bipartido 9

9(8). Láminas acintadas, anchas, de (1–)1.4–1.5 cm de ancho . . . . *A. pennellii*

9′. Láminas angostamente lineares, de 1.2–6 mm de ancho 10

10(9). Inflorescencias formadas por (5–)11–17(–30) racimos; plantas medianamente robustas, láminas de 20–40(–60) cm de largo; cañas plurinodes (5–6 nudos) . . . . *A. polydactylus*

10′. Inflorescencias con 2–6(–10) racimos; plantas gráciles, láminas de (1–)12–25 cm de largo; cañas paucinodes o plurinodes 11

11(10). Raquis de los racimos con pelos largos (1–2 mm de largo), dispersos sobre los ángulos o bien concentrados a la altura de la base de los pedicelos 12

11′. Raquis de los racimos glabros, con los márgenes escabriúsculos 13

12(11). Hojas concentradas en la base de la planta, rectas, ascendentes; raquis con pelos dispersos a lo largo de los ángulos, más numerosos en la base de los pedicelos; espiguillas densamente distribuidas a lo largo del raquis, de 0.6–0.8 mm de ancho; gluma superior y lemma inferior iguales o mayores que el antecio, 2(3)-nervias . . . . *A. elegantulus*

12′. Hojas dispuestas a lo largo de las cañas, principalmente en la porción media e inferior, con las vainas imbricadas; láminas arcuadas; raquis con pelos concentrados sólo a la altura de la base de los pedicelos; espiguillas laxamente dispuestas a lo largo del raquis, de 0.5–0.6 mm de ancho; gluma superior menor que el antecio, lemma inferior igual al mismo, ambas 2(–4)-nervias . . . . *A. arcuatus*

13(11). Gluma superior y lemma inferior, 0.1–0.4 mm más largas que el antecio, 4–5-nervias 14

13′. Gluma superior menor que el antecio, rara vez igual, 2-nervia, lemma inferior igual o mayor que el antecio, 2–3-nervia 15

14(13). Cañas 2(–3)-nodes; nudos vilosos; espiguillas de 1.9–2.5 mm de largo, gluma superior y lemma inferior 4(–5) nervias, con pelitos delgados a ambos lados de los nervios; Panamá . . . . *A. jeanyae*

14′. Cañas plurinodes (10 ó más nudos); nudos glabros; espiguillas de 2.6–2.8(–3) mm de largo, gluma superior y lemma inferior 4-nervias, glabras; Venezuela . . . . *A. gracilis*

15(13). Espiguillas de 2–2.2 mm de largo, cortamente pilosas, con pelos delicados, adpresos, sobre toda la superficie de la gluma superior y lemma inferior; espiguillas distribuidas laxamente a lo largo del raquis, las contiguas oponen 0–1/4 de su longitud; pedicelos de 0.4–0.6 mm de largo; Belice . . . . *A. ciliatifolius*

15′. Espiguillas de 1.6–1.7(–1.8) mm de largo, densamente pilosas, con pelos rígidos a lo largo de los márgenes y hacia la base de la espiguilla junto al pedicelo, el resto de la superficie esparcidamente pilosa; espiguillas distribuidas más densamente sobre el raquis, las contiguas opuestas en 1/4 o más de su longitud; pedicelos de 0.1–0.2 mm de largo; Brasil . . . . *A. hoehnei*

1. Axonopus arcuatus (Mez) G. A. Black, Advancing Frontiers Pl. Sci. 5: 137. 1963. Basónimo: *Paspalum arcuatum* Mez, Repert. Spec. Nov. Regni Veg. 15: 60. 1917. TIPO: Brasil. Minas Gerais, sin loc., Ago. 1889, *A. F. M. Glaziou 17933* (holotipo, B no visto; isotipos, BAA 2033! fragm. ex P, G-DEL no visto, K!, foto ex K en SI!, P no visto, US 2941983! fragm. ex B).

Plantas perennes, gráciles, de 0.40–0.60 m de altura, rizomatosas, el rizoma corto, densamente cespitosas; cañas delgadas de 2 mm de diámetro, simples, levemente comprimidas, plurinodes, lisas, con surco lateral conspicuo, glabras; nudos castaños, comprimidos, glabros; vainas menores que los entrenudos, conspicuamente estriadas, pajizas o castañas, glabras, con bordes lisos, hialinos, glabros; nervios de las vainas se continúan en la lámina; cuello levemente conspicuo, castaño, o bien inconspicuo, pajizo, glabro, con numerosos pelos hacia los márgenes de la vaina; lígulas membranáceo-ciliadas, de 0.3–0.4 mm, castañas, blanquecinas en el márgen; contralígula y aurículas ausentes; láminas arqueadas, rígidas, 6–10 × 0.2–0.45 cm, concentradas en la base y zona media de la planta, plegadas en la base, luego planas, con bordes planos, el ápice agudo u obtuso, la base continuándose imperceptiblemente con la vaina, longitudinalmente estriadas en ambas caras, hipofilo glabro, a veces con pelos dispersos, más frecuentes sobre el nervio medio cerca del ápice, epifilo levemente escabriúsculo, con los márgenes escabriúsculos, a veces también con pelos delgados, ralamente dispuestos, más cercanos y numerosos hacia la base. Cañas floríferas con 1 inflorescencia terminal subdigitada, con pedúnculo cilíndrico, ligeramente comprimido, longitudinalmente estriado, con surco lateral conspicuo, glabro; inflorescencia formada por 4–6(–8) racimos de 5.5–9(–12) cm; raquis de los racimos recto a levemente ondulado, triquetro, cara dorsal plana, cara ventral con costilla conspicua, de 0.3–0.5 mm de ancho, castaño y con tintes violáceos, hispídulo sobre los ángulos y con pelos largos de 1.5–2 mm en la base de los pedicelos; pedicelos aplanados, 0.1–0.2 mm, escabriúsculos en los ángulos, con numerosos pelos largos similares a los del raquis. Espiguillas de contorno oblongo-elíptico, de 1.7–2.1(–2.3) × 0.5–0.6 mm, dorsiventralmente comprimidas, agudas, ocráceas, alternas y laxamente distribuidas en 2 hileras a lo largo del raquis, de tal manera que cada espiguilla resulta opuesta a una de la otra hilera en

1/4–1/3 de su longitud; gluma superior y lemma inferior frecuentemente tan largas como el antecio, gluma superior a veces algo menor, con ápice agudo, membranáceo-hialinas, ambas 2(–4)-nervias, con los nervios marginales, glabras; lemma superior oblongo-elíptica, 1.6–2 mm, castaña, brillante, glabra, con densas y pequeñas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y lisos, encerrando los bordes de la pálea; pálea superior similar a la lemma, ligeramente menor, glabra. Cariopsis no vista.

Distribución geográfica y ecología. Conocida sólo para el estado de Minas Gerais, Brasil.

Fenología. Coleccionada en flor y/o fruto desde agosto hasta febrero.

Black (1963) menciona que *Axonopus arcuatus* se halla relacionado a *A. polydactylus*, distinguiéndolas principalmente por sus caracteres vegetativos. Anton (1982) señala que *A. arcuatus* podría tratarse de un ejemplar empobrecido de *A. polydactylus*. Sin embargo, es posible diferenciar a *A. polydactylus* por incluir plantas de mayor porte, de (0.5–)0.9–1.2 m de altura, mayor cantidad de racimos, de (5–)11–17(–30), éstos de 7.5–18(–23) cm de largo y sus láminas rectas, no curvas. Consecuentemente, en este trabajo se mantienen como especies independientes.

Axonopus arcuatus es también afín a *A. elegantulus*, coleccionada en los Andes de Perú, distinguiéndose esta última especie por presentar hojas ascendentes, rectas, concentradas en la base de la planta, espiguillas distribuidas más densamente a lo largo del raquis, éstas más anchas (0.6–0.8 mm de ancho) y por presentar pelos largos, dispersos sobre los ángulos del raquis y en la base de los pedicelos.

Mez (1917) menciona "Brasilia" como lugar de colección, sin especificar localidad. En la foto del isotipo depositado en K se indica "Minas", probablemente refiriéndose al estado de Minas Gerais, y en la etiqueta del isotipo depositado en BAA dice "campos de Itabirá, 21 Nov. 1888".

Material examinado. BRASIL. **Minas Gerais:** Serra do Itabirito, ca. 50 km SE of Belo Horizonte, *Irwin et al. 19768* (US).

2. **Axonopus argentinus** Parodi, Notas Mus. La Plata, Bot. 3(17): 15. 1938. TIPO: Argentina. Entre Ríos: Dpto. Concordia, Concordia, Ene. 1922, *L. R. Parodi 4649* (holotipo, BAA 300!; isotipos, IAN no visto, SI!, US 1723532!). Figuras 1A–C, 3.

Axonopus argentinus var. *glabriflorus* Parodi, Notas Mus. La Plata, Bot. 3(17): 19. 1938. TIPO: Uruguay. Salto, Ene. 1937, *G. Orihuela 60, Herb. Mus. Nac. Montevideo 5038* (holotipo, BAA 302!; isotipos, MVM no visto, US 2236050! fragm. ex BAA).

Axonopus argentinus var. *glabripes* Parodi, Notas Mus. La Plata, Bot. 3(17): 19. 1938. *Axonopus argentinus* subsp. *glabripes* (Parodi) Roseng., B. R. Arrill. & Izag., Gram. Urug. 293. 1970. TIPO: Argentina. Entre Ríos: Dpto. Concordia, Pedermar [Pedernal], Mayo 1933, *J. Friedermann 60* (holotipo, BAA 303!; isotipo, IAN no visto).

Axonopus argentinus f. *hirsutus* Parodi, Notas Mus. La Plata, Bot. 3(17): 18. 1938. TIPO: Argentina. Entre Ríos: Dpto. Concordia, Concordia, Feb. 1930, *L. R. Parodi 9584* (holotipo, BAA 305!; isotipo, IAN no visto).

Axonopus suffultus (Mikan ex Trin.) Parodi var. *pubiflorus* Parodi, Notas Mus. La Plata, Bot. 3(17): 23. 1938. *Axonopus argentinus* Parodi subsp. *pubiflorus* (Parodi) Roseng., B. R. Arrill. & Izag., Gram. Urug. 293. 1970. TIPO: Uruguay. Montevideo: Sayago, 22 Dic. 1921, *L. R. Parodi 91* (holotipo, BAA 334!; isotipos, foto ex BAA en SI!, IAN no visto, SI!, US 1127741!).

Axonopus hagenbeckianus (Kuntze) Parodi var. *pratensis* G. A. Black, Advancing Frontiers Pl. Sci. 5: 141. 1963. TIPO: Brasil. Rio Grande do Sul: Porto Alegre, Morro da Gloria, 26 Oct. 1945, *B. Rambo 29313* (holotipo, US 1910224!; isotipos, foto ex US en SI!, LIL no visto).

Axonopus paraguayensis G. A. Black, Advancing Frontiers Pl. Sci. 5: 135. 1963. TIPO: Paraguay. Paraguarí: Caapucú, Estancia Barrerito, Ene. 1949, *T. Rojas 13103a* (holotipo, US 2012988!; isotipos, foto ex US en SI!, K!).

Axonopus ramboi G. A. Black, Advancing Frontiers Pl. Sci. 5: 134. 1963. Syn. nov. TIPO: Brasil. Rio Grande do Sul: Cambará, 30 Ene. 1948, *B. Rambo 36460* (holotipo, US 1935537!; isotipos, foto ex US en SI!, K!).

Plantas perennes, cespitosas, de 0.2–1 m de altura, con rizomas delgados, estoloniformes, falciformes o rectos, cubiertos por numerosos catáfilos coriáceos; innovaciones intravaginales y extravaginales; cañas delgadas a ligeramente robustas aplanadas, de 2–3 mm diámetro, simples, 2–3-nodes, pajizas, longitudinalmente estriadas, con surco lateral conspicuo, glabras o con pelos en el surco lateral, o ralamente vilosas en los entrenudos a densamente vilosas hacia los nudos, con pelos de 3–4 mm de largo; nudos castaños, levemente comprimidos, glabros a pubérulos, a veces vilosos; vainas menores que los entrenudos, conspicuamente estriadas, pajizas, glabras o con algunos pelos largos en el borde hacia el cuello, a densamente vilosas, generalmente más notable cerca del cuello; nervios de las vainas continúandose en la lámina; cuello distinguible, castaño, glabro a piloso; lígulas membranáceas, de 0.5–1 mm, con márgen densamente pestañoso, el resto de la superficie glabra; aurículas y contralígula ausentes; láminas lineares, rígidas, de 10–30(–40) × 0.3–0.7 cm, predominantemente basales en la planta, plegadas en la base, planas hacia el ápice, la base continuándose imperceptiblemente con la vaina, el ápice obtuso o agudo, con pequeño acúmen algo punzante, glabras o con escasos pelos sobre el nervio medio en el epifilo, los márgenes glabros o escabriúsculos, o con escasos pelos de 2.5–3 mm cerca de la base o en toda su

Figura 3. *Axonopus argentinus* Parodi (de *Schinini 14606*, SI). —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción del raquis. —D. Espiguilla vista del lado de la gluma superior. —E. Espiguilla vista del lado de la lemma inferior. —F. Antecio superior visto del lado de la lemma. —G. Antecio superior visto del lado de la pálea.

extensión, nervio central y laterales conspicuos. Cañas floríferas con 2 ó 3 inflorescencias de desarrollo desigual, naciendo del último nudo caulinar, cada una de ellas con pedúnculo aplanado, glabro, longitudinalmente estriado; inflorescencia más desarrollada con (3–)5–10(–15) racimos de (6–)10–12(–18) cm, siendo los basales alternos levemente distantes entre sí y los apicales más cercanos; raquis de los racimos notablemente ondulado, pajizo o con tintes violáceos, triquetro, cara dorsal plana, de 0.5–0.75 mm de ancho, cara ventral con costilla conspicua, hispídulo, más conspicuamente sobre los ángulos, generalmente con 1–4 pelos largos de 1.5–2 mm, blanquecinos, más o menos rígidos situados sobre los ángulos a ambos lados de la base de cada pedicelo; pedicelos muy breves, de 0.2–0.3 mm, conspicuamente aplanados, escabriúsculos en los ángulos, ocasionalmente con algunos pelos largos similares a los del raquis. Espiguillas de contorno oblongo-elíptico, de 1.9–3 × 0.6–1 mm, dorsiventralmente comprimidas, ocráceas, más raramente con tintes purpúreos, glabras a cortamente pilosas, alternas, dispuestas en 2 hileras a lo largo del raquis, de tal forma que cada espiguilla se opone a otra de la otra hilera en 1/3–1/2 de su longitud; gluma superior y lemma inferior de 1.9–3 mm, membranáceo-hialinas, con el ápice cortamente acuminado a subagudo, glabras o con escasos pelos delgados dispersos, a veces más densos hacia la base, los bordes y el ápice, 2(–4)-nervia, con los nervios próximos al márgen; lemma superior elíptica, 1.8–2.4 mm, endurecida, castaña, subigual o hasta 0.6 mm más corta que la gluma superior y la lemma inferior, poco brillante, glabra, con escasos pelitos cortos en el ápice; lemma con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente menor que la lemma, glabra; estambres 3, anteras purpúreas de 1–1.5 mm. Cariopsis elipsoide, de 1.5 × 0.6 mm, blanquecina; hilo oblongo, subbasal; embrión 1/2 del largo de la cariopsis.

Distribución geográfica y ecología. Habita el sudeste y sur de Brasil (estados de Paraná, Rio Grande do Sul y Santa Catarina), Paraguay (en la región oriental y occidental), Uruguay (Departamentos de Flores, Florida, Cerro Largo, Durazno, Lavalleja, Montevideo, Paysandú, Salto, Tacuarembó y Treinta y Tres) y la Argentina (Provincias de Chaco, Corrientes, Entre Ríos, Misiones y Santa Fe). Esta especie es común en bordes de montes, campos semihúmedos o en suelos arenoso-rocosos más secos.

Fenología. Coleccionada en flor y/o en fruto entre los meses de octubre y mayo.

Nombre vulgar. "Kapi'ipe ñu" (Paraguay; Morrone et al., 1994).

Número cromosómico. $n = 10, 20$ (Hickenbick et al., 1975, sub *Axonopus ramboi*).

Axonopus argentinus es afín a *A. suffultus* y *A. pressus*. *Axonopus suffultus* se distingue por tener rizomas de entrenudos cortos, no hojosos, vainas glaucas y cuello indistinguible. *Axonopus pressus* se aparta por incluir plantas más robustas, de 0.7–1.5(–2) m de altura, con gruesas innovaciones, comprimidas, cubiertas por vainas dísticas y pajizas, láminas acintadas, de (10–)20–45 × 0.8–1.2 cm, rígidas, frecuentemente bipartidas en el ápice cuando viejas, inflorescencias mayores, de (10–)20–45 cm y racimos de (10–)13–32 cm.

Parodi (1938: 19) al describir *Axonopus argentinus* var. *glabriflorus* indica como material tipo "Montevideo n° 5038, Salto, leg. *Orihuela n° 60*, 1–1937". En los herbarios BAA y SI se halló otro ejemplar, no citado en el protólogo, en cuya etiqueta se indica: "Herb. Museo Nacional Montevideo 5038, *J. Arechavaleta s.n.*".

Black (1963) describe a *Axonopus ramboi* sobre la base del ejemplar *Rambo 36460* y lo diferencia de otras especies de la serie por sus espiguillas mayores, de 2.7–2.9 mm y antecio superior 0.3–0.5 mm más corto que la gluma superior y lemma inferior. El análisis de la descripción original, del material tipo y del material de herbario de *A. argentinus* permitió confirmar que existe una marcada variación en el tamaño de la espiguilla (de 1.9–3 mm) y en el largo relativo de la gluma superior y la lemma inferior en relación al antecio superior, desde subiguales hasta 0.6 mm más largas. Además, el material tipo de *A. ramboi* depositado en el herbario US posee rizomas delgados, alargados cubiertos por numerosos catáfilos coriáceos, típicos de *A. argentinus*. Por todas estas razones, *A. ramboi* se incluye en la sinonimia de *A. argentinus*.

Longhi-Wagner et al. (2001), al tratar el género *Axonopus* para São Paulo, Brasil, sigue el concepto de Black (1963) y considera a *A. ramboi* como una especie válida, y señala que la especie posee la gluma superior y lemma inferior 5-nervia. Sin embargo el análisis del material tipo permitió comprobar que ambas son 2-nervias.

Axonopus argentinus es una especie que presenta una marcada variabilidad en el porte de las plantas, en la pilosidad de las vainas, láminas y pedicelos y en el tamaño de las hojas y de los racimos de las inflorescencias, razón por la cual se han considerado bajo esta especie numerosos taxones infraespecíficos (Parodi, 1938; Burkart, 1968; Rosengurtt et al., 1970; Anton, 1982). El análisis de material de herbario permitió confirmar que existe una continua gradación

en los caracteres anteriormente mencionados que no permite la diferenciación de taxones discretos.

Rosengurtt et al. (1970) señalan que *Axonopus argentinus* es un forrajera medianamente apetecida por el ganado.

Material adicional examinado. ARGENTINA. **Chaco:** Dpto. 1 de Mayo, Colonia Benítez, *Schulz 11786* (BAA), *Schulz 3269* (BAA). **Corrientes:** Dpto. Capital, *de Llames s.n.* (BAA 5460); Dpto. Concepción, Est. Santillán, Rincón de Luna, *Pedersen 4482* (BAA); Dpto. Gral. Alvear, Alvear, *Meyer 32* (BAA); Dpto. Ituzaingó, Ruta 12 próximo a Ituzaigó, *Nicora & Cámara Hernández 517* (BAA); 10 km NNE de Ituzaingó, camino a Guardia Cué, *Quarín et al. 1850* (LPB); Dpto. Mburucuyá, sin loc., *Pedersen 6426* (BAA); Est. Santa María, *Pedersen 5876* (BAA); Dpto. Mercedes, Mercedes, *Parodi 6191, 6359* (BAA); Est. Ñu-Porá, *Martínez Crovetto 9940* (BAA); Dpto. Montes Caseros, sur de Combai, *Nicora 571* (BAA); Dpto. San Roque, *Sarli 101* (BAA); Est. Caaguarí, *Pedersen 5829* (BAA); Chavarría, junto a la Ruta 123, *Quarín et al. 4137* (CTES, SI). **Entre Ríos:** Dpto. Colón, Ayo. Palmar, *Burkart et Crespo 22922* (BAA, SI); Dpto. Concordia, Colonia Yeruá, *Galli 54* (BAB, SI), *Galli 287* (SI); Dpto. Concordia, Concordia, *Baez 27* (BAA); Santa Ana, *Burkart et Troncoso 26193* (SI), *Cabrera 28268* (SI); Dpto. La Paz, Banderas, Est. La Esperanza, *Burkart et Bacigalupo 21023* (SI); sin loc., *Baez s.n.* (BAA 6436); Dpto. Paraná, Hernandarias, *Burkart et al. 25270* (SI); Dpto. Uruguay, Concepción del Uruguay, Est. Río Uruguay, cerca de Gualeguaychú, *Burkart 24078* (BAA, SI). **Misiones:** Dpto. Apóstoles, Campo San Juan, *Fontana F 111-6* (SI); Dpto. Capital, Posadas, Establecimiento Santa Inés, *Parodi 4632* (BAA); Dpto. Guaraní, Ruta Prov. 2, Reserva Ecológica Provincial, *Morrone et al. 720* (SI). **Santa Fe:** Dpto. Capital, Santo Tomé, *Parodi 157* (BAA); Gral. Obligado, Camino de Reconquista a Dr. Barros Pasos, *Job 760* (BAA).

BRASIL. **Paraná:** Castro, *Araujo 33* (BAA). **Rio Grande do Sul:** S. Sebastião do Cai, Faz. Paquete, *Araujo 175* (BAA, US); Montenegro, *Araujo 102* (BAA); Pelotas, *Swallen 9169* (US). **Santa Catarina:** Mun. Lajes, Rio Bandeirinhas, 23 km N of Lajes, *Smith & Klein 8237* (US); Mun. Pórto União, *Smith & Klein 8629* (US); Mun. Iraní, Campo de Iraní, *Smith & Klein 13990* (US). **São Paulo:** depósito de remonta de São Simão, *del Mazzo 25* (BAA).

PARAGUAY. **Alto Paraná:** Puerto Casado, *Ramírez 649* (US). **Amambay:** Pedro Juan Caballero, Sierra de Amambay, *Rojas 6701* (BAA). **Central:** San Lorenzo del Campo Grande, Escuela Mariscal Estigarribia, *Rojas 14105* (LIL, US); "Paraguaria centralis, in regione lacus Ypacaray", *Hassler 12556* (G, US). **Cordillera:** Tobatí, Cerro Cabayú, entre rocas, *Rojas 5254* (BAA, SI). **Guairá:** Villarrica, *Rojas 14076* (BAA, SI); Iturbe, *Montes 12834* (BAA); Camino entre Villa Rica y Coronel Oviedo, *Rua et al. 38* (BAA). **Paraguarí:** Est. Barrerito, Caápucú, *Rojas 13129* (BAA, LIL); Parque Nacional Ybicuí, campo cerrado on Ayo. Minas basin, 5 km N of adm. area, *Zardini 11827* (MO). **Presidente Hayes:** Chaco, frente a Asunción, *Rojas 5432* (BAA, SI).

URUGUAY. **Canelones:** Dpto. 1° de Mayo, Parque Centenario, *Rosa-Mato 1463* (BAA). **Cerro Largo:** Río Negro, entre losayos, Palleros y Areguá, *Rosengurtt 1063* (BAA, US); Río Negro, Palleros, *Gallinal et al. 1491* (US). **Durazno:** Maestre Campo, *Dauber 111* (BAA). **Flores:** Río Jí, *Rosengurtt B-588* (BAA, US). **Florida:** Río Jí y Ayo. Manzavillagra, *Rosengurtt B-715* (BAA); F. C. Cerro Colorado, Est. Sta. Elvira, *Rosengurtt 305* (US). **Lavalleja:** Est. Pororó, *Pedersen 3638* (BAA). **Montevideo:** Montevideo, *Arechavaleta s.n.* (BAA 301, SI). **Paysandú:** Costa del Río Uruguay, *Lombardo 3032* (BAA). **Salto:** Río Uruguay y Ayo. San Antonio Grande, *Rosengurtt B-955* (BAA). **Sin departamento:** Río Uruguay, *Orihuela 63* (BAA).

3. Axonopus ciliatifolius Swallen, J. Wash. Acad. Sci. 23: 458. 1933. TIPO: Belice. El Cayo Dist.: Mtn. Pine Ridge, 25 Feb. 1931, *H. H. Bartlett 11746* (holotipo, US 1503594!; isotipos, foto ex US en SI!, K!, MO 3701229!). Figura 4.

Plantas perennes, conspicuamente cespitosas, de 0.50–0.70 m de altura, con rizomas breves, engrosados y cubiertos por las catáfilas, con numerosas raíces adventicias y vástagos aéreos; cañas gráciles de 2–3 mm diámetro, simples, levemente aplanadas, con surco lateral conspicuo, 2–3-nodes, pajizas, longitudinalmente estriadas, glabras; nudos castaños, glabros; vainas menores que los entrenudos, conspicuamente estriadas, pajizas, totalmente glabras o con algunos pelitos dispersos sobre la cara externa, con los bordes lisos, glabros; nervios de las vainas se continúan en la lámina; cuello inconspicuo; lígulas membranáceas, 0.1–0.3 mm, pajizas, blanquecinas y densamente pestañosas hacia el borde; aurículas y contralígula ausentes; láminas angostamente lineares, rígidas, (5–)12–14(–25) × 0.1–0.2 cm, predominantemente basales, plegadas en la base, luego planas, de ápice acuminado, la base continuándose imperceptiblemente con la vaina, longitudinalmente estriadas en ambas caras, con nervio central y laterales conspicuos, con pelos delgados y largos, de base tuberculada, más densamente dispuestos hacia el borde. Cañas floríferas con 2 a 4 inflorescencias naciendo del último nudo caulinar, cada una de ellas con pedúnculo aplanado, glabro, longitudinalmente estriado; inflorescencia formada por 2 a 6 racimos de 3–12 cm; raquis de los racimos levemente sinuoso, triquetro, cara dorsal plana, de 0.2–0.5 mm de ancho, cara ventral con costilla conspicua, pajizo en la zona central y verdoso hacia los laterales, hispídulo, más conspicuamente sobre los ángulos, sin pelos largos; pedicelos aplanados, ensanchados hacia el ápice, 0.4–0.6 mm, hispídulos. Espiguillas de contorno oblongo-elíptico, 2–2.2 × 0.8–0.9 mm, dorsiventralmente comprimidas, ocráceas, alternas, laxamente dispuestas en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a una de la otra hilera en 0–1/4 de su longitud; gluma superior y lemma inferior membranáceo-hialinas, 2–2.2 mm, gluma superior menor que el antecio, rara vez igual o mayor, obtusa, lemma inferior igual o levemente mayor que el antecio, aguda, ambas 2-nervias, ocasionalmente 3-nervias, los nervios conspicuos, glabras o con pelitos delgados, delicados, dispersos sobre toda la superficie; lemma

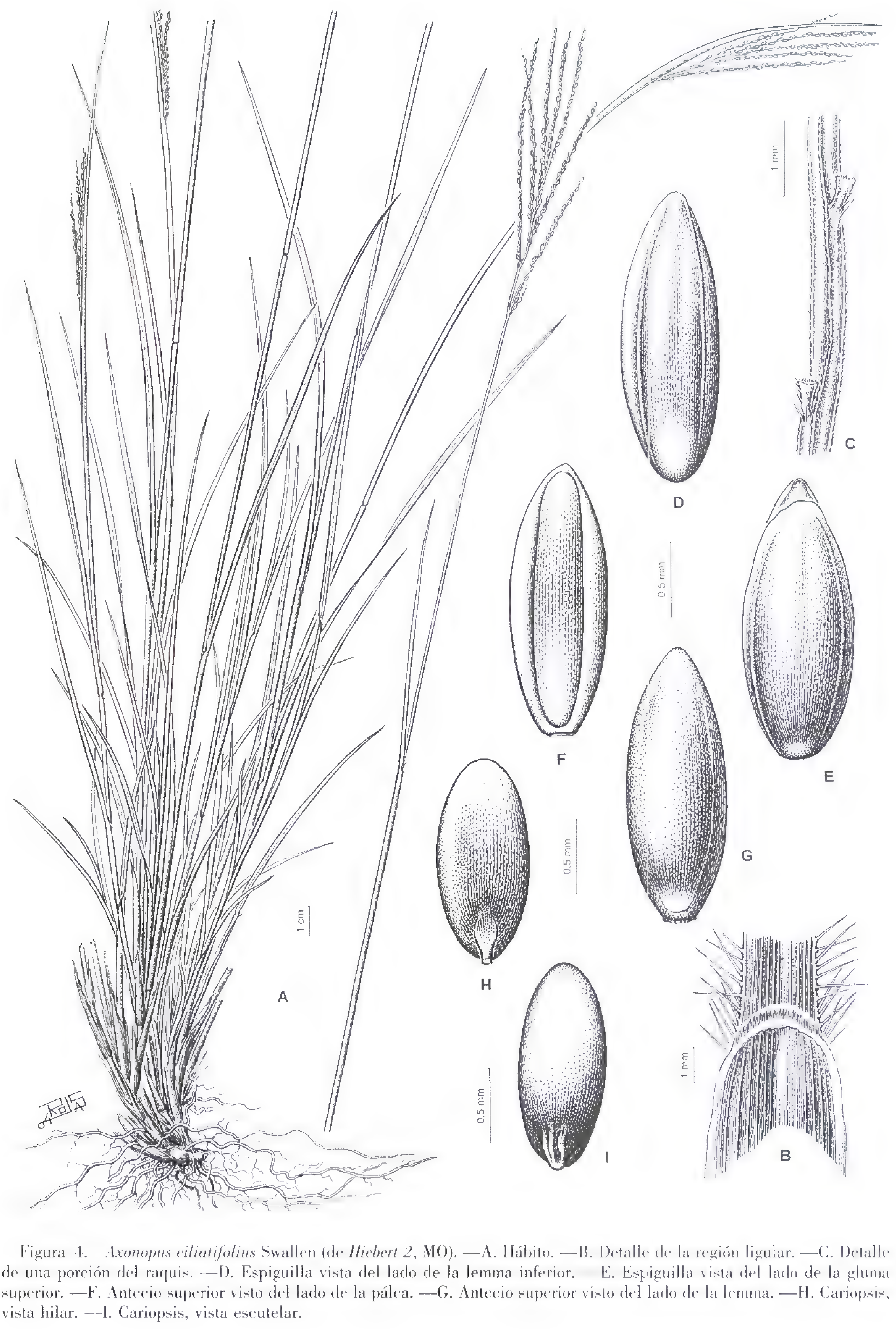

Figura 4. *Axonopus ciliatifolius* Swallen (de *Hiebert 2*, MO). —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción del raquis. —D. Espiguilla vista del lado de la lemma inferior. —E. Espiguilla vista del lado de la gluma superior. —F. Antecio superior visto del lado de la pálea. —G. Antecio superior visto del lado de la lemma. —H. Cariopsis, vista hilar. —I. Cariopsis, vista escutelar.

superior elipsoide, ca. 2.1 mm, castaña, lustrosa, glabra, con escasos pelitos cortos en el ápice, con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente menor que la lemma, glabra. Cariopsis no vista.

Distribución geográfica y ecología. Hasta el momento sólo es conocida para El Cayo, Belice. Habita en savanas montanas, ocasionalmente sujetas a fuegos periódicos, entre los 600–800 m.

Fenología. Hallada en flor y/o en fruto entre los meses de agosto y febrero.

Axonopus ciliatifolius presenta, junto con *A. elegantulus*, *A. arcuatus*, *A. jeanyae*, *A. gracilis* y *A. hoehnei*, hábito grácil, hojas con láminas angostas e inflorescencias con pocos racimos. *Axonopus elegantulus* y *A. arcuatus* se apartan por la presencia de pelos en el raquis; *A. jeanyae* y *A. gracilis* se distinguen por tener la gluma superior y la lemma inferior mayores que el antecio, 4–5-nervias; finalmente, *A. hoehnei*, hasta el momento especie endémica del norte de Brasil, se diferencia de *A. ciliatifolius* por sus espiguillas menores (1.6–1.7 mm de largo) y sus pedicelos más cortos (0.1–0.2 mm de largo).

Black (1963) relaciona *Axonopus ciliatifolius* con *A. poiophyllus* Chase, esta última perteneciente a la serie Axonopus, distinguiéndola principalmente por sus antecios pálidos. *Axonopus poiophyllus* además presenta hojas más anchas, de 2–4(–8) mm de ancho, espiguillas mayores, de 2.5–3.5 mm de largo y gluma superior y lemma inferior mayores que el antecio, 2–4-nervias.

Material examinado. BELICE. **Belize:** Almost border of Stann Creek Distr., along Manatee (Coastal) Hwy, 7.4 mi. S of turnoff to Gales Point, *Nee & Atha 46906* (MO). **Cayo:** Mt. Pine Ridge, along No. 2 Line Rd., near Augustine, *Hiebert 36* (MO); Mt. Pine Ridge, Blancaneaux Lodge, *Wiley 475* (MO); Mt. Pine Ridge, along A-10, For. Res., 200 yds. above Rio Frio Crossing, *Hiebert 2* (MO).

4. Axonopus cuatrecasasii G. A. Black, Advancing Frontiers Pl. Sci. 5: 147. 1963. TIPO: Colombia. Arauca: Los Llanos, Río Casanare, Esmeralda, 130 m, woods sabana, 19–20 Oct. 1938, *J. Cuatrecasas 3882* (holotipo, US 1797918!; isotipo, foto ex US en SI!). Figura 5.

Plantas perennes, de 50–120 cm de altura, gráciles, ligeramente cespitosas, estoloníferas, con estolones delgados; cañas delgadas de 2 mm de diámetro, rectas o geniculadas, simples, cilíndricas, con surco lateral ligeramente conspicuo, 2- a 4-nodes, a veces ramificadas en los nudos basales, pajizas, longitudinalmente estriadas, glabras en los entrenudos; nudos castaños, levemente comprimidos, densamente vilosos en toda la superficie del nudo o bien solo en su base; vainas menores o de igual largo que los entrenudos, longitudinalmente estriadas, glabras a vilosas en su cara externa, a veces solo los bordes y el nervio medio densamente vilosos hacia el cuello; nervios de las vainas se continúan en la lámina; cuello diferenciado, con una línea castaña, glabro, a veces viloso hacia los bordes; lígulas membranáceo-ciliadas, castañas, de 0.2–0.5(–1) mm, pubescentes, blanquecinas; aurículas y contralígula ausentes; láminas lineares, rígidas, 15–23(–32) × 0.3–0.5 cm, predominantemente basales en la caña, plegadas en la base, luego planas, con bordes planos, ápice agudo, de base continuándose imperceptiblemente con la vaina, longitudinalmente estriada en ambas caras, hipofilo glabro a densamente viloso, epifilo glabro o con pelos ralos a densos, los bordes densamente vilosos hacia la base de la lámina, luego hispídulos a escabriúsculos. Cañas floríferas con 1 a 2 inflorescencias subdigitadas en la última vaina foliar, con pedúnculo cilíndrico, levemente comprimido, con surco lateral notable, longitudinalmente estriado o liso, glabro; inflorescencia compuesta por (3–)5–6(–9) racimos delgados, de (5.5–)7.5–10.5(–16) cm; raquis de los racimos recto a muy levemente ondulado, triquetro, cara dorsal plana, de 0.4–0.7 mm de ancho, cara ventral con costilla conspicua, pajizo, glabro o con pelitos cortos, escabriúsculo sobre los ángulos; pedicelos aplanados, 0.1–0.2 mm, glabros. Espiguillas de contorno oblongo-elíptico, de (1.5–)1.7–2 × 0.7–0.8 mm, agudas, dorsiventralmente comprimidas, ocráceas, espaciadamente distribuídas en 2 hileras a lo largo del raquis, de tal manera que cada espiguilla se opone a una de la otra hilera en (1/2–)1/3 o menos de su longitud; gluma superior y lemma inferior subiguales, tan largas como la espiguilla, glabras o con escasos pelitos a los lados de los nervios y los márgenes, 2-nervias, con los nervios submarginales, ocasionalmente 4-nervias, con los nervios subiguales, tenues, muy poco manifiestos; lemma superior elíptica, 1.6–1.9 × 0.6–0.7 mm, castaña, brillante, glabra, con densas y pequeñas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y lisos, encerrando los bordes de la pálea; pálea superior similar a la lemma, levemente menor, glabra; estambres 3, anteras de 1–1.2 mm. Cariopsis no vista.

Distribución geográfica y ecología. Venezuela (Estados Anzoátegui, Monagas, Yaracuy), Colombia (Departamento de Arauca) y Bolivia (Departamento Santa Cruz). Crece en sabanas, en suelos arenosos, bien drenados, entre los 100 y los 1000 m.

Fenología. Coleccionada en flor y/o en fruto entre los meses de agosto y abril.

Figura 5. *Axonopus cuatrecasasii* G. A. Black (de *Renvoize & Cope 3994*, MO). —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción del raquis. —D. Espiguilla vista del lado de la gluma superior. —E. Espiguilla vista del lado de la lemma inferior. —F. Antecio superior visto del lado de la lemma. —G. Antecio superior visto del lado de la pálea.

Axonopus cuatrecasasii se caracteriza por incluir plantas cespitosas con cañas estoloníferas, que arraigan en los nudos basales y originan nuevas plantas, los nudos son pilosos, el cuello distinguible con una línea castaña y el ápice de las láminas largamente agudo. El raquis de las ramificaciones es glabro, marcadamente triquetro con la quilla muy desarrollada protegiendo a las espiguillas.

Black (1963) al describir la especie señala que las espiguillas son glabras. El análisis del material de herbario permitió observar una marcada variabilidad en la pilosidad de la espiguilla, encontrándose ejemplares con espiguillas glabras (*Montes 1304a*), cortamente pilosas, con pelos delicados dispuestos en dos líneas a lo largo de las nervaduras y los márgenes de la gluma superior y lemma inferior (*Renvoize & Cope 4029*, *Montes 1305-A*) o glabras y pilosas en un mismo ejemplar (*Killeen 1577* y *1725*, *Steinbach 1979*, *Renvoize & Cope 3994*).

Renvoize (1998) menciona en la descripción de *Axonopus cuatrecasasii* que la gluma superior y lemma inferior son 4-nervias. El estudio del material tipo y de ejemplares de herbario (entre ellos el citado por el autor, *Killeen 1725*) permitió determinar que la gluma superior y la lemma inferior son 2-nervias, y muy ocasionalmente se hallaron espiguillas con la gluma superior y la lemma inferior 4-nervias, los nervios siempre cercanos al margen, siendo los más externos poco conspicuos.

Material adicional examinado. BOLIVIA. **Santa Cruz:** Prov. Cordillera, 50 km S of Santa Cruz, *Renvoize & Cope 3947* (LPB, US); Chiquitos, Est. San Ignacio, 22 km N of San José, *Killeen 1725* (LPB, SI, US); Andrés Ibañez, W of Santa Cruz to Montero Hwy, just S of turnoff to Viru Viru Airport, *Nee 36379* (LPB); Andrés Ibañez, Las Lomas de Arena, 10 km E of YPFB refinery, *Killeen 1577* (LPB, SI); Andrés Ibañez, large sand dunes S of the town, *Renvoize & Cope 4029* (LPB, MO, US); Santa Cruz to Montero, near Viru Viru, *Renvoize & Cope 3994* (LPB, MO, US).

VENEZUELA. **Anzoátegui:** Vecindad de Santo Tomé, *Sandoval s.n.* (US 1764950); Sabanas de Trachipogon, con árboles diseminados, El Piñal, 3 km NE de San Diego de Cabrutica, *Montes 1304a* (MO); alrededores del Hato La Iguana, Santa María de Ipire, *Montes 1305a* (MO). **Monagas:** sandy flat along Rio Purgatorio, *Chase 12596* (US). **Yaracuy:** 4 km N of Salom, *Davidse et al. 20754* (MO, US).

5. Axonopus elegantulus (J. Presl) Hitchc., Contr. U.S. Natl. Herb. 24: 433. 1927. Basónimo: *Paspalum elegantulum* J. Presl, Reliq. Haenk. 1: 211. 1830. TIPO: Perú, sin loc., sin fecha, *T. Haenke s.n.* (holotipo, PR no visto; isotipos, B no visto, BAA 310!, US 2854680! fragm. ex B).

Paspalum attenuatum J. Presl, Reliq. Haenk. 1: 212. 1830. *Axonopus attenuatus* (J. Presl) Hitchc., Contr. U.S. Natl. Herb. 22(6): 471. 1922. TIPO: Perú. Huánuco, *T. Haenke s.n.* (holotipo, PR no visto; isotipos, MO 2101073!, MO 939545!, US 2854681! fragm. de procedencia no indicada).

Paspalum gregoriense Mez, Bot. Jahrb. Syst. 56: 10. 1921. TIPO: Perú. Huancavelica: Prov. Tayacaja, linke Talwand des Flusses Mantaro, über San Gregorio, 1300–1400 m, 4 Abr. 1913, *A. Weberbauer 6570* (holotipo, B no visto; isotipos, foto ex B en US 2854682!, BAA 2156! fragm. ex B, US 2854682!, US 1498088!).

Plantas perennes, gráciles, de 0.25–0.75 m de altura, cespitosas, rizomatosas; cañas delgadas de 2 mm de diámetro, simples, 2- ó 3-nodes, longitudinalmente estriadas, levemente comprimidas, con surco lateral conspicuo, glabras; nudos castaños, comprimidos, glabros, a veces con algunos pelos; vainas menores que los entrenudos, conspicuamente estriadas, pajizas, cara externa con pelos blanquecinos, cortos y delgados, ralos, adpresos, cara interna glabra, con los bordes lisos, glabros a densamente vilosos; nervios de las vainas se continúan en la lámina; cuello conspicuo, con pelos hacia los márgenes; lígulas membranáceo-pestañosas, de 0.4–0.5 mm, castañas en la base, luego pajizas, con borde blanquecino; contralígula y aurículas ausentes; láminas lineares, rígidas, de 7–15 × 0.2–0.25(–0.6) cm, predominantemente basales en la planta, plegadas en la base, luego planas, los bordes planos a levemente revolutos, el ápice agudo o cortamente acuminado, retuso, hendido en hojas viejas, longitudinalmente estriadas en ambas caras, glabras, con los márgenes escabriúsculos, en ocasiones pilosos hacia la base. Cañas floríferas con 1 inflorescencia terminal subdigitada, con pedúnculo cilíndrico, ligeramente comprimido, longitudinalmente estriado, con surco lateral menos conspicuo que en las cañas, glabro; inflorescencia formada por 3–6(–10) racimos de 6–11(–13) cm, siendo los basales alternos y distantes, los apicales más próximos entre sí; raquis de los racimos ondulado, pajizo, triquetro, cara dorsal plana, de 0.4–0.5 mm de ancho, cara ventral con costilla conspicua, glabra o con algunos pelos cortos, escabriúsculo y con pelos largos, 1–2 mm, rígidos, dispersos sobre los ángulos, más densos cerca de la base de los pedicelos; pedicelos muy breves, ca. 0.2 mm, aplanados, escabriúsculos en los ángulos, con algunos pelos largos similares a los del raquis. Espiguillas de contorno elíptico, de 1.8–2.1 × 0.6–0.8 mm, dorsiventralmente comprimidas, agudas o subagudas, ocráceas, alternas y densamente distribuidas en 2 hileras a lo largo del raquis, de tal forma que cada espiguilla resulta opuesta a una de la otra hilera en 1/3–1/2 de su longitud; gluma superior y lemma inferior tan largas como el antecio, con ápice cortamente acuminado, membranáceo-hialinas, con tintes violáceos, gluma superior 2–3-nervia, cuando 3-nervia el nervio medio a veces solo notable hacia el

ápice, lemma inferior 2-nervia, ambas glabras; lemma superior oblongo-elíptica, 1.7–2.1 mm, castaña, brillante, glabra, escabrosa en el ápice, excepcionalmente sin escabrosidades, con densas y pequeñas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y lisos, encerrando los bordes de la pálea; pálea superior similar a la lemma, ligeramente menor, glabra. Cariopsis no vista.

Distribución geográfica y ecología. Habita en los andes de Perú entre los 1000–3400 m, sobre suelos descubiertos y rocosos.

Fenología. Encontrada con flores y/o frutos entre los meses de diciembre y abril (junio).

Axonopus elegantulus es similar a *A. arcuatus*, distinguiéndose esta última especie por tener las hojas arcuadas, dispuestas en la zona basal y media de la planta, por sus racimos gráciles, delgados y por las espiguillas de ápice agudo, más angostas (0.5–0.6 mm de ancho) y más espaciadas en el raquis, resultando opuestas solamente en 1/4–1/3 de su longitud. En *A. elegantulus*, en cambio, las hojas se encuentran concentradas en la base de la planta, los racimos son de aspecto más robusto y más compacto, por la densa disposición de las espiguillas a lo largo del raquis, opuestas en 1/3–1/2 de su longitud.

Axonopus elegantulus también puede confundirse con *A. polydactylus*, distinguiéndose esta última especie por sus cañas plurinodes, sus láminas de 20–60 cm de largo, el raquis con frecuencia hispídulo, el número de los racimos frecuentemente entre 11 y 17 y la distribución más laxa de las espiguillas a lo largo del raquis.

En el herbario US existe una cartulina con detalladas anotaciones de Chase, que además incluye un duplicado de un ejemplar depositado en B y otro en PR con los siguientes datos "Paspalum pulchellum nov. sp., inéd., Peruvia, Haenke". Este nombre no fue publicado válidamente por Presl. Chase indica que en Praga no encontró el material tipo determinado por Presl como *Paspalum elegantulum*. Sin embargo señala que los especímenes de B y PR determinados como *P. pulchellum* con letra de J. Presl concuerdan con el protólogo de *P. elegantulum*. De acuerdo con Chase, en este trabajo se considera que los ejemplares mencionados depositados en US corresponden a la colección tipo de *P. elegantulum*. Un isotipo de la misma colección se halla depositado en BAA.

Mez (1921), al describir *Paspalum gregoriense*, considerado sinónimo de *Axonopus elegantulus* por Hitchcock (1927), señala que las espiguillas son de 1.5 mm. El análisis del material tipo permitió determinar que las espiguillas miden 1.9–2 mm.

Tovar (1993) considera a *Axonopus attenuatus* como un taxón independiente de *A. elegantulus*, distinguiéndola por el mayor número de racimos (8–11) y las espiguillas de menor tamaño (1.6–2 mm de largo). El estudio del material tipo y de ejemplares de herbario de ambas especies permite confirmar que existe una continuidad en los caracteres mencionados y que se trata de una misma entidad. Asimismo se observó que la pilosidad del raquis es marcadamente variable, desde conspicuamente piloso a lo largo de los ángulos, como en los ejemplares *Hutchinson & Wright 3962*, *Tovar 1407* y *Macbride 3324*, hasta esparcidamente piloso, con pelos dispuestos más densamente en la base de los pedicelos (en *Kunkel 623*, *Macbride 3760*, *Asplund 13556* y *Fosberg 27824*); excepcionalmente el raquis puede presentar muy escasos pelos a la altura de la base de los pedicelos, como en el ejemplar *van der Werff et al. 8406* y *Tovar 188*. De acuerdo con Anton (1982), *A. attenuatus* representaría un extremo de *A. elegantulus* con espiguillas menores, más distanciadas y pedicelos menos pilosos.

Hitchcock (1922, 1927) cita la presencia de *Axonopus elegantulus* (bajo *A. attenuatus*) para Guyana, sin embargo los materiales citados por este autor corresponden a *A. flabelliformis*.

Jørgensen y Ulloa (1994) y Zuloaga y Morrone (1999) citan erróneamente a *Axonopus elegantulus* para Ecuador sobre la base del ejemplar *Acosta Solís 20497* (US), material que por sus características pertenece a la serie Barbigeri (sensu Black, 1963), y corresponde a *A. scoparius*. Black (1963) cita *A. elegantulus* para Loja, Ecuador, mencionando el ejemplar *Espinosa 308* depositado en el herbario de US. El mismo no ha podido ser localizado por lo que la presencia de esta especie en Ecuador debe ser confirmada.

Material examinado. PERÚ. **Amazonas:** Bongara, betw. Río Utcubamba and Shipasbamba, 4 km from Campo. Ingenio, *Hutchison et Wright 3962* (MO, US). **Apurimac:** Grau, Hda. Secosecka, *Vargas 5746* (MO, US); Abancay, Ampay, Tamburco, al N de Abancay, *Nuñez et Vargas 7230* (MO). **Cajamarca:** Hda. Sondor, Namora, *Sánchez Vega 177* (US); Jaen, Tabaconas, on Rio Tabaconas, 20 km Huancabamba, *Fosberg 27824* (MO). **Cuzco:** 20 km N of Ollantaytambo, *Hitchcock 22515* (NY, US). **Huancavelica:** Mejorada, *Tovar 1407* (MO); Prov. Huancavelica, Checcyancu, a 4 km E de Conaica, *Tovar 188* (US). **Huánuco:** Prov. Pachitea, Panao, *Asplund 13556* (US). **Junin:** Huancayo, *Soukup 1905* (MO, US), *Soukup 3977* (US), *Kunkel 623* (BAA); Huancayo, mtns. behind city of Huancayo, *Black 46-696* (US). **Pasco:** Oxapampa, Palmazo, Coop. Navarra, *van der Werff et al. 8406* (MO, US). **Sin departamento:** Mito, *Macbride 3270* (US), *Macbride 3324* (US), *Macbride et Featherstone 1498* (US); Yanano, *Macbride 3760* (US).

6. Axonopus flabelliformis Swallen, Bull. Torrey Bot. Club 75: 82. 1948. TIPO: Guyana. Halfway station betw. Wismar and Rockstone, Demerara River, in sandy soil, 30 Dic. 1919–Ene. 1920, *A. S. Hitchcock 17275* (holotipo, US 1038571!; isotipo, foto ex US en SI!). Figuras 1D, 6.

Axonopus purpurellus Swallen, Bull. Torrey Bot. Club 75: 83. 1948. TIPO: Surinam. Km 68, vic. ectie O, on wet sandy soil, 19 Oct. 1944, *B. Maguire & G. Stahel 24997* (holotipo, US 1713731; isotipos, foto US 1914999!, NY no visto, foto ex NY en SI!).

Axonopus kaietukensis Swallen, Bull. Torrey Bot. Club 75: 83. 1948. TIPO: Guyana. Kaieteur Savannas, locally frequent, rocky dry ground, 14 May 1944, *B. Maguire & D. B. Fanshawe 23454* (holotipo, US 1713871; isotipos, foto ex US en SI!, F no visto, NY-346104!, foto US 1914991!).

Axonopus tamayonis Luces, Bol. Soc. Venez. Ci. Nat. 15(80): 21. 1953. TIPO: Venezuela. Bolívar, Gran Sabana, Santa Elena, en el cerro Okurimá, 11 Feb. 1946, *F. Tamayo 2747* (holotipo, VEN 93794!; isotipos, foto ex VEN en US!, F no visto, MO!, US 1910959!, US 3049572!).

Axonopus flabelliformis var. *camporum* G. A. Black, Advancing Frontiers Pl. Sci. 5: 145. 1963. TIPO: Guayana Francesa. Est. Sinnamary to Iracoubo, km 13, campo, 29 Oct. 1954, *G. A. Black & R. M. Klein 54-17390* (holotipo, IAN no visto; isotipos, CAY no visto, US 2303305!, foto ex US en SI!).

Axonopus flabelliformis var. *decipiens* G. A. Black, Advancing Frontiers Pl. Sci. 5: 146. 1963. TIPO: Surinam. Poika Savanna, 4 July 1951, *A. T. Semple 381* (holotipo, US 2184143!).

Plantas perennes, cespitosas, de 0.55–1(–2) m de altura, con rizoma corto y robusto, cubierto por vainas fibrosas; cañas generalmente aplanadas de 2–4 mm de diámetro, 2- ó 3-nodes, simples, longitudinalmente estriadas, glabras, cubiertas por las vainas basales equitantes; nudos castaños, levemente comprimidos, glabros a densamente vilosos; vainas conspicuamente estriadas, pajizas, glabras a vilosas, con frecuencia más densamente cerca del margen y hacia el cuello, dispuestas en forma notablemente dística, conduplicadas, comprimidas lateralmente, de manera que las láminas quedan dispuestas en 2 hileras, el conjunto de aspecto flabeliforme; nervios de las vainas se continúan en la lámina; cuello imperceptible; lígulas membranácea-pestañosas, brevísimas, ca. 0.3 mm, castaño rojizo, con margen blanquecino; contralígula y aurículas ausentes; láminas lineares, rígidas, 10–20(–60) × 0.5–0.9 cm, dispuestas en la base y porción mediana de las cañas, plegadas en toda su longitud o solamente en la base y planas hacia el ápice, de ápice subagudo u obtuso, base continua con la vaina, longitudinalmente estriadas en ambas caras, con nervio central y laterales conspicuos, glabras en ambas caras o bien escabriúsculas en el epifilo y densamente vilosas en el hipofilo, con los márgenes lisos, glabros o hispídulos hacia el ápice, o con escasos pelos de 2.5–3 mm cerca de la base o en toda su extensión. Cañas floríferas con 1–3 inflorescencias, naciendo en el último nudo caulinar, pedúnculos cilíndricos o aplanados, longitudinalmente estriados, glabros; inflorescencia con 6–20(–30) racimos de 5–15(–20) cm, los basales en ocasiones ramificados, alternos levemente distantes entre sí y los apicales simples, más cercanos; raquis de los racimos notablemente ondulado a casi recto, pajizo en la zona central, verdoso en los márgenes, triquetro, cara dorsal plana, (0.3–)0.6–0.8(–1.3) mm de ancho, cara ventral con costilla conspicua, hispídulo en toda su superficie, más conspicuamente sobre los ángulos, sin pelos largos, o con pelos de 1–1.5 mm, situados sobre los ángulos a ambos lados de la base de algunos pedicelos; pedicelos de (0.1–)0.2–1 mm, conspicuamente aplanados, glabros a pubérulos. Espiguillas de contorno oblongo-elíptico, (1.3–)1.6–2.2 × 0.6–0.7 mm, dorsiventralmente comprimidas, ocráceas, alternas, dispuestas en 2 hileras a lo largo del raquis, de tal forma que cada espiguilla se opone a otra de la otra hilera en 0–2/3 de su longitud; gluma superior de 1.2–1.5(–2.2) mm, generalmente menor que el antecio, obtusa, muy rara vez igual y aguda, 2-nervia, ocasionalmente 3-nervia, glabra o pubescente con algunos pelitos cortos a ambos lados de los nervios; lemma inferior de 1.3–2 mm, membranáceo-hialina, ligeramente menor o tan larga como el antecio, 2-nervia, glabra o pubescente; lemma superior de 1.6–1.8 mm, aguda, castaña, poco brillante, glabra, ocasionalmente con escasos y cortos pelitos en su ápice, con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente menor que la lemma, glabra. Cariopsis no vista.

Número cromosómico. $n = 20$ (Hickenbick et al., 1975, sub *Axonopus flabelliformis* var. *camporum*).

Distribución geográfica y ecología. Bolivia (La Paz), Brasil (Amazonas y Roraima), Guyana, Guayana Francesa, Surinam y Venezuela (Bolivar y T.F. de Amazonas). Judziewicz (1990) la cita también para los estados de Pará y Amapá, Brasil, mientras que Giraldo-Cañas (1999) la menciona para Colombia, en el departamento Meta. Crece en sabanas abiertas, sobre suelo arenoso, o entre rocas emergentes, entre los 100–1600 m.

Fenología. Coleccionada en flor y/o fruto durante todo el año.

Esta especie es fácilmente reconocible por la disposición marcadamente equitante de sus vainas basales.

Axonopus flabelliformis es afín a *A. polydactylus*, distinguiéndose esta última especie por la disposición de sus vainas basales alrededor de las cañas, no equitante. Asimismo, en *A. polydactylus* la gluma superior es mayor que el antecio y el ápice de los antecios es usualmente cortamente escabroso, mien-

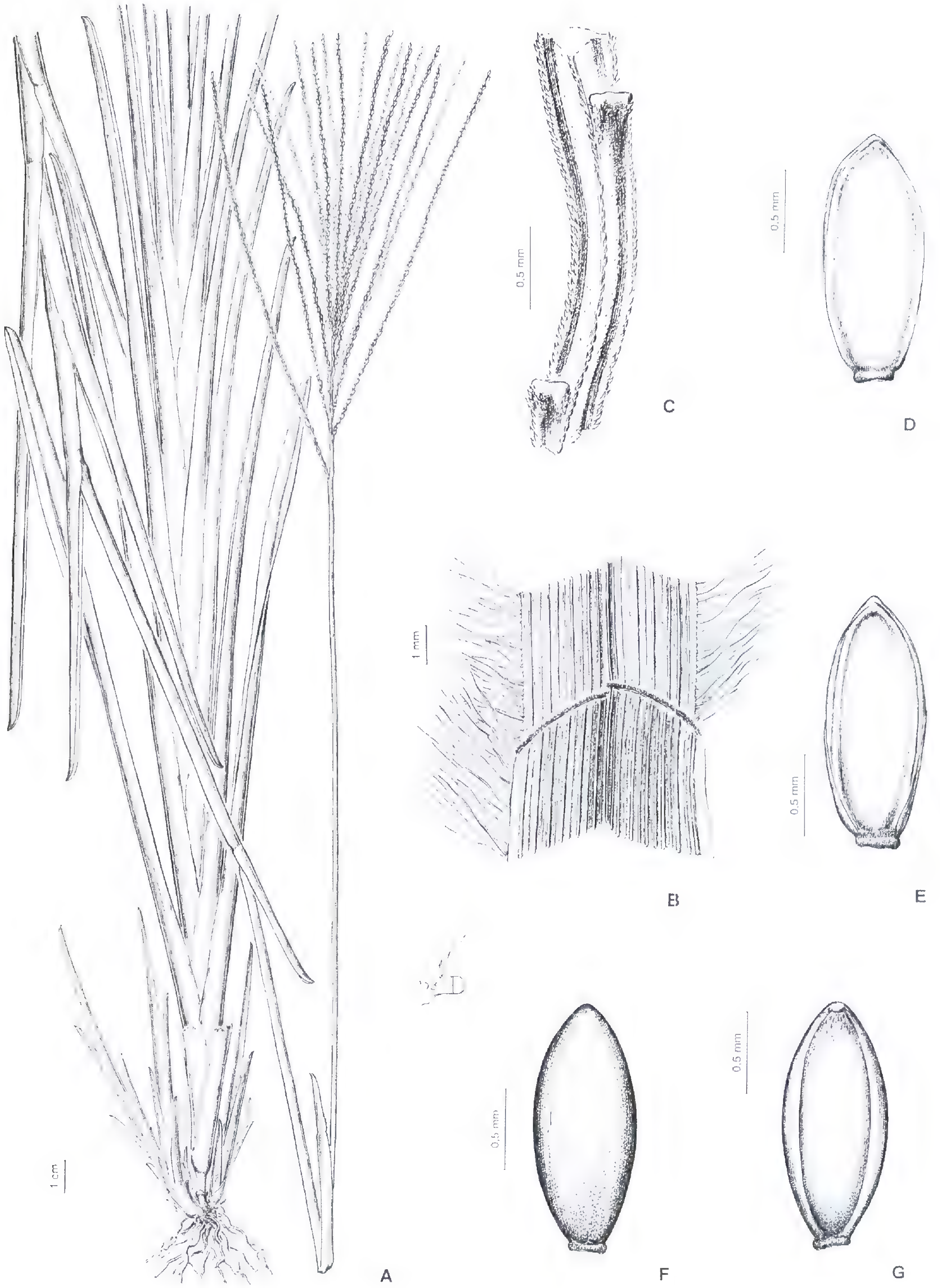

Figura 6. *Axonopus flabelliformis* Swallen (de *Harrison & Persaud 1049*, NY). —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción del raquis. —D. Espiguilla vista del lado de la gluma superior. —E. Espiguilla vista del lado de la lemma inferior. —F. Antecio superior visto del lado de la lemma. —G. Antecio superior visto del lado de la pálea.

tras que en *A. flabelliformis* la gluma superior es menor que el antecio y el antecio superior es liso.

Axonopus flabelliformis también se halla estrechamente relacionada a *A. magallanesiae*, principalmente por la disposición equitante de las vainas. Sin embargo, *A. magallanesiae* es una planta más pequeña (hasta de 50 cm de altura), presenta inflorescencias compuestas por pocos racimos (3–5), de 4–8 cm, sus espiguillas son más grandes, de 2.2–2.4(–2.5) mm, y la gluma superior y la lemma inferior son 4–5-nervias, con los nervios laterales conspicuos.

Black (1963) reconoce dentro de *Axonopus flabelliformis* tres variedades: la variedad tipo, la variedad *camporum* caracterizada por tener espiguillas esparcidamente pilosas y la variedad *decipiens* por presentar las vainas ligeramente equitantes, raquis de los racimos con dos a cinco pelos y espiguillas pequeñas (de 1.3–1.4 mm). El análisis del material tipo y de herbario en general permitió determinar que existe una marcada variabilidad en los caracteres morfológicos anteriormente mencionados y por tal razón estas variedades se incluyen en la sinonimia de *A. flabelliformis*.

Axonopus flabelliformis var. *decipiens* fue incluida en la sinonimia de *A. polydactylus* por Anton (1982). Al estudiar un fragmento del holotipo de la primera, se comprobó que el raquis es más ancho, de 0.9–1 mm versus 0.3–0.4 mm en *A. polydactylus*, carácter que permite sinonimizarla con *A. flabelliformis*.

Por otra parte, *Axonopus purpurellus* fue considerada sinónimo de *A. polydactylus* por Anton (1982). El estudio del holotipo de *A. purpurellus* permitió comprobar que las vainas basales son fuertemente equitantes y el raquis de los racimos también es más ancho que en *A. polydactylus* (0.7–1 mm de ancho). Por las características anteriormente mencionadas se considera que *A. purpurellus* debe incluirse en la sinonimia de *A. flabelliformis*, coincidiendo con el criterio de Judziewicz (1990) y de Zuloaga y Morrone (2003).

Swallen (1948) al describir *Axonopus kaietukensis* señala que se halla estrechamente relacionada a *A. flabelliformis*, diferenciándola por las espiguillas más grandes (2 mm vs. 1.6 mm), las láminas más largas (15–20 cm vs. 9–15 cm) y las vainas más cortas y con márgenes densamente vilosos. Del análisis del material tipo de *A. kaietukensis* se pudo comprobar que el rango de las espiguillas es de 1.6–2 mm, siendo este caracter continuo con lo observado en *A. flabelliformis*. Además, como se indicó anteriormente, las dimensiones de las láminas y de las vainas, asi como la pilosidad de estas últimas no son caracteres válidos para separar ambos taxones.

Black (1963) y Renvoize (1998) citan bajo *Axonopus elegantulus* el ejemplar *Buchtien 12* coleccionado en La Paz, Bolivia, depositado en BAA, IAN y US. Sin embargo, el estudio de un duplicado de dicho ejemplar procedente de MO, permitió confirmar que las vainas basales son marcadamente equitantes, carácter que, junto con los numerosos racimos, permite identificarlo como *A. flabelliformis*. Black (1963) menciona que en el mencionado material las espiguillas inmaduras son pilosas, mientras que las maduras son glabras. Se ha podido observar que las espiguillas maduras presentan densos pelos tuberculados en la gluma superior y la lemma inferior y antecios castaños.

De acuerdo con Judziewicz (1990) y Anton (1982) esta especie es marcadamente polimorfa en cuanto la pilosidad de las vainas, de los raquis y de las espiguillas. Un ejemplo de esta variabilidad, se observó en el ejemplar *Williams 1000*, procedente de La Paz, Bolivia, el cual consta de dos plantas, una de ellas con espiguillas glabras y la otra con espiguillas pilosas.

Las inflorescencias de *Axonopus flabelliformis* ocasionalmente presentan ramificaciones en la base de los racimos inferiores, característica que fue observada en *Hoock 412*, *Maguire & Fanshawe 32621* y *Boerboom 8764*.

Material adicional examinado. BOLIVIA. **La Paz:** Prov. Tamayo, Senda Apolo–San José de Uchupiamonas a media hora antes de llegar a Naranjai, *Miranda et al. 732* (LPB); Prov. Tamayo, near Apolo, *Smith 1000* (NY); Prov. Larecaja, San Carlos, San José, Mapiri Region, *Buchtien 12* (BAA, MO).

BRASIL. **Amazonas:** Tunui, Rio Icana, *Luetzelburg 22410* (R-50055); Icana, no planalto da cachoeira, *Luetzelburg 22954* (R). **Roraima:** Serra Tepequem, *Maguire et Maguire 27* (US).

GUAYANA FRANCESA. Rte. Sinnamary, km 14–15, *Hoock 410a* (US), *Hoock 412* (US), *Hoock 414a* (US), *Hoock 420a* (VEN).

GUYANA. **Cuyuni-Mazaruni Region:** 7 km N Paruima village, after descent from S face, Mt. Waleliwatipu, *Mc Dowell et Hughs 2972* (US); Pakaraima Mtns., basecamp 8.6 km NE Imbaimadai on Partang R. tributary, 0.5 km N, *Hoffman et al. 1781* (US); Linden Hwy., near turnoff to St. Cuthbert's Mission, *Gillespie et al. 753* (US). **Essequibo Isl-W Demerara Region:** S of Georgetown on Soesdyke–Linden Hwy., ca. 7 mi. N of Loo River, *Peterson & Gopaul 7459* (US). **Mahaica-Berbice Region:** St. Cuthbert's Mission road cut-off, 2 km E of the Timahri–Linden Hwy., *Judziewicz & Lall 5410* (US). **Potaro-Siparuni Region:** Kaieteur Nat. Park, 1 km W from W end of airstrip, *Henkel & Williams 2309* (US); Savanna at S base of Mt. Kopinang along trail from Kopinang to Orinduik, *Hahn et al. 4428* (US). **Waranama Ranch:** Berbice River, *Harrison & Persand 1049* (NY, US).

SURINAM. Nat. Res. "Brinchheuvel", *Teunissen et Wildschut 11548* (US); Sabakoe Savannah, *Hoock s.n.* (US); Savanna sectio O, *Pulle 141* (US); Zanderij savanne, westzijde, *Geyskes 128* (US); Zanderij I, *Hoock 1268* (US); Blahawatra, near Yodensavanne, *Boerboom LBB8764* (US); Poika Savannah, *Semple 381* (US); Sabakoe Savannah, *Hoock 1265* (US).

VENEZUELA. **Amazonas:** Dpto. Atures, al W del medio Río Asita, *Huber 3523* (VEN); Dpto. Atabapo, 10 km al W de la Serranía Asisa, *Huber 6217* (VEN). **Bolívar:** Rocío, entre San Francisco de Yuruaní y Chirimatá, ca. 10–15 km al ENE de San Ignacio de Yuruaní, *Huber 9162* (MO); Dist. Rocío, 7.5 km al NW de Santa Elena de Uairén, *Steyermark & Liesner 127569* (VEN); Gran Sabana, Parq. Nac. Canaima, Kama-Meru, 109 km de Tumeremo pasando por El Dorado, Río Kama, *Morrone et al. 4761* (SI); 7 km N of La Ciudadela, *Davidse et al. 4942* (VEN); Cumbre de Cerro Guaiquinima, a lo largo del Río Szczerbanari, *Steyermark & Dunsterville 113164* (VEN); Mun. Sucre, *Delgado 1108* (VEN).

7. Axonopus gracilis G. A. Black, Mem. New York Bot. Gard. 9: 254. 1957. TIPO: Venezuela. Amazonas: Cerro Sipapo (Paráque), SE ridge and savanna slopes, infrequent, 1700 m, 20 Dic. 1948, *B. Maguire & L. Politi 27818* (holotipo, NY no visto, foto SI! ex NY; isotipo, US 2236051! fragm. ex NY).

Plantas perennes, cespitosas, ca. 1 m de altura, con rizomas delgados y cortos; cañas aplanadas de 2.5–3 mm de ancho, simples, plurinodes, pajizas, longitudinalmente estriadas, glabras; nudos castaños, glabros; vainas conspicuamente estriadas, pajizas, con tintes rosados hacia el ápice, los bordes hialinos, lisos, glabras; cuello inconspicuo; lígulas membranáceas, 0.2–0.4 mm, con márgen densamente pestañoso, el resto de la superficie glabra; nervios de las vainas se continúan en la lámina; aurículas y lígula externa o contralígula ausentes; láminas lineares, rígidas, 1–30 × 0.1–0.4 cm, predominantemente basales, plegadas, planas hacia el ápice, de ápice agudo, base continua con la vaina, sin pseudopecíolo, longitudinalmente estriadas en ambas caras, con nervio central y laterales conspicuos, glabras, con margen escabriúsculo, viloso en la zona basal. Cañas floríferas con 1 ó 2 inflorescencias, cada una de ellas con pedúnculo aplanado, glabro, longitudinalmente estriado; inflorescencias con 3–4 racimos de 4–12 cm, siendo los basales alternos levemente distantes entre sí y los apicales más cercanos; raquis de los racimos ondulado, triquetro, violáceo o verdoso, cara dorsal plana, 0.3–0.4 mm de ancho, cara ventral con costilla conspicua, escabriúsculo, más conspicuamente sobre los ángulos; pedicelos muy breves, hasta de 0.2 mm de largo, aplanados, escabriúsculos en los ángulos. Espiguillas de contorno oblongo-elíptico, 2.6–2.8(–3) × 0.7–0.9 mm, dorsiventralmente comprimidas, obtusas o cortamente apiculadas, ocráceas, alternas, dispuestas en 2 hileras sobre el raquis; gluma superior y lemma inferior mayores que el antecio, 2.6–3 mm, membranáceo-hialinas, 4-nervias, los nervios cercanos a ambos márgenes, rara vez con nervio central apenas conspicuo, glabras; lemma superior de 2.5–2.8 mm de largo, castaña, poco brillante, glabra, con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente menor que la lemma, glabra. Cariopsis no vista.

Distribución geográfica y ecología. Especie poco frecuente, hasta el momento es conocida por la colección tipo del Cerro Sipapo (Venezuela), en sabanas a 1700 m.

Fenología. Hallada en flor y/o fruto en el mes de diciembre.

Esta especie fue considerada bajo la sinonimia de *Axonopus polydactylus* (Anton, 1982; Zuloaga & Morrone, 2003). Sin embargo, *A. gracilis* posee inflorescencias formadas por 3–4 racimos, de 4–12 cm, espiguillas de 2.6–2.8(–3) mm, gluma superior y lemma inferior 4-nervias, con el nervio medio ausente. *Axonopus polydactylus*, en cambio, tiene (5–)11–17(–30) racimos, de 7.5–18(–23) cm, las espiguillas son de 1.2–1.6(–2.3) mm, la gluma superior es 2(3)-nervia y la lemma inferior es 2-nervia.

Black (1963) considera a *Axonopus gracilis* dentro de la serie Axonopus. No obstante por las características de su hábito y por la morfología de la espiguilla, esta especie debe incluirse dentro de la serie *Suffulti*, coincidiendo con el criterio adoptado por Giraldo-Cañas (2000a).

8. Axonopus hoehnei G. A. Black, Advancing Frontiers Pl. Sci. 5: 143. 1963. TIPO: Brasil. Pará: Lageado, Rio Tapajóz, Feb. 1912, *F. C. Hoehne 5310 (134)* (holotipo, IAN no visto; isotipo, US 22366057! fragm. ex IAN).

Plantas perennes, levemente cespitosas, de 0.50–0.60(–1.25) m de altura, con rizomas breves y delgados; cañas cilíndricas, de 1–2 mm de diámetro, 2- ó 3-nodes, simples, gráciles, pajizo verdoso, longitudinalmente estriadas, con surco lateral poco notable, glabras; nudos castaños, glabros; vainas menores que los entrenudos, conspicuamente estriadas, castañas, glabras, de bordes lisos; nervios de las vainas se continúan en la lámina; cuello conspicuo, glabro, con una línea triangular, castaña a ambos lados del márgen; aurículas y contralígula ausentes; lígulas membranáceas, cortamente pestañosas en el borde, de 0.1–0.3 mm, castaño rojizo, el borde blanquecino; láminas angostamente lineares, rígidas, 10–15 × 0.3–0.4 cm, predominantemente basales, plegadas en la base, la base continua con la vaina, planas hacia el ápice, éste largamente acuminado, longitudinalmente estriadas en ambas caras, con nervio central y laterales conspicuos, glabras. Cañas floríferas con 1–2 inflorescencias naciendo del último

nudo caulinar, cada una de ellas con pedúnculo delgado y aplanado, glabro, longitudinalmente estriado; inflorescencia formada por 4–8(–13) racimos de 7–10 cm; raquis sinuoso, pajizo, triquetro, cara dorsal plana, 0.7–0.8 mm de ancho, cara ventral con costilla conspicua, híspido, más conspicuamente sobre los ángulos, sin pelos largos; pedicelos de 0.1–0.2 mm, híspidos, aplanados, ensanchados hacia el ápice. Espiguillas de contorno oblongo-elíptico, de 1.6–1.7(–1.8) × 0.7–0.9 mm, dorsiventralmente comprimidas, ocráceas, alternas, dispuestas en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a otra de la otra hilera en 1/4 de su longitud; gluma superior y lemma inferior membranáceo-hialinas, 1.6–1.8 mm, gluma superior menor que el antecio, obtusa, rara vez igual, lemma inferior igual que el antecio, aguda, ambas 2(–3)-nervias, los nervios conspicuos, con pelitos delgados, rígidos, dispersos sobre toda la superficie, principalmente hacia ambos lados de los nervios y más densamente hacia la base; lemma superior de 1.5–1.7 mm, castaña, lustrosa, glabra, con micropelos bicelulares y con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente menor que la lemma, glabra. Cariopsis no vista.

Distribución geográfica y ecología. Hasta el momento sólo es conocida para estado de Pará, Brasil. Crece en lugares bajos, periodicamente inundados, sobre suelos arenosos, y asociados a arbustos y pequeños árboles entre los 400–500 m.

Fenología. Coleccionada en flor y/o fruto entre los meses de diciembre y febrero.

Zuloaga y Morrone (2003), siguiendo el criterio de Anton (1982), tratan a *Axonopus hoehnei* bajo la sinonimia de *A. pennellii*. Anton (1982) considera que ambas entidades serían dos variantes locales de una misma especie, meramente distintas en el grado de pubescencia que presentan las partes vegetativas. Sin embargo, *A. hoehnei* presenta hojas con láminas lineares de 10–15 cm × 3–4 mm, rígidas, con vainas de dorso subredondeado, cuello distinguible con una región triangular castaña, inflorescencias con raquis más ancho (0.6–0.8 mm de ancho) y espiguillas obtusas, pilosas, con pelos distribuidos principalmente hacia ambos lados de los nervios y más densamente hacia la base. Consecuentemente, en este trabajo se mantiene a *A. hoehnei* como un taxón independiente de *A. pennellii*.

Axonopus hoehnei resulta también afín a *A. ciliatifolius*, distinguiéndose esta última especie por su hábito densamente cespitoso, sus pedicelos mayores (0.4–0.6 mm de largo) y sus espiguillas más grandes (2.1–2.2 mm de largo). Hasta el presente, *A. ciliatifolius* ha sido coleccionada sólo en Belice.

Material examinado. BRASIL. **Pará:** Serra do Cachimbo, *Pires et al. 6156a, 6178* (US); region of Missão Velha, a Mundurukú village, ca. 2 km N of the Rio Curuá, *Anderson 10908* (MO).

9. Axonopus jeanyae Davidse, Ann. Missouri Bot. Gard. 74: 421. 1987. TIPO: Panamá. Coclé, area betw. Caño Blanco del Norte, Caño Sucio and Chorro del Río Tife, evergreen forest, 200–400 m, spray basin of waterfall, 3 Feb. 1983, *G. Davidse & C. W. Hamilton 23570* (holotipo, MO 3475959!; isotipos, foto ex MO en SI!, ISC no visto, PMA no visto, US 3260346!). Figura 1E.

Plantas perennes, gráciles, cespitosas, de 50–75 cm de altura, con rizomas cortos y delgados; cañas delgadas, 2(–3)-nodes, simples, pajizas, longitudinalmente estriadas, glabras; nudos negruzcos, vilosos; vainas menores que los entrenudos, estriadas, pajizas, totalmente glabras, ciliadas en el margen; nervios de las vainas se continúan en la lámina; cuello inconspicuo; lígulas membranáceo-ciliadas, ca. 0.5 mm; aurículas y contralígula ausentes; láminas lineares, rígidas, hasta de 25 × 0.2–0.3 cm, predominantemente basales, plegadas en toda su longitud o planas hacia el ápice, de ápice obtuso, escabroso, base continua con la vaina, longitudinalmente estriadas en ambas caras, glabras o papiloso-ciliadas hacia la base. Cañas floríferas generalmente con 2 inflorescencias en el último nudo caulinar, cada una de ellas con pedúnculo delgado, glabro, longitudinalmente estriado; inflorescencia con 2–5 racimos de 4–11 cm, siendo los basales alternos levemente distantes entre sí y los apicales más cercanos; raquis levemente ondulado, pajizo verdoso, triquetro, cara dorsal plana, 0.4–0.6 mm de ancho, cara ventral con costilla conspicua, escabroso, sin pelos largos; pedicelos de 0.2–0.5 mm, lisos, glabros. Espiguillas de contorno oblongo-elíptico, de 1.9–2.5 × 0.7–0.8 mm, dorsiventralmente comprimidas, ocráceas, alternas, dispuestas laxamente en 2 hileras sobre el raquis, de tal forma que cada espiguilla no se opone a otra de la otra hilera; gluma superior y lemma inferior membranáceo-hialinas, 1.9–2.5 mm, ambas mayores que el antecio, 4–5-nervias, con pelitos delgados a ambos lados de los nervios; lemma superior de 1.8–2.4 mm, castaña, brillante, con escasos pelitos cortos en el ápice de la lemma, con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente

menor que la lemma, glabra; estambres 3, anteras de 1–1.5 mm, purpúreas. Cariopsis no vista.

Distribución geográfica y ecología. Sólo ha sido encontrada en Panamá, entre los 200 y los 400 m, en lugares húmedos, asociados a caídas de agua.

Fenología. Hallada en flor y/o fruto en el mes de febrero.

Axonopus jeanyae resulta afín a *A. ciliatifolius*, especie hasta el momento endémica de Belice. Esta última se distingue por sus nudos glabros, los nervios de la gluma superior y la lemma inferior son menos conspicuos, la gluma superior es 2-nervia y menor que el antecio, rara vez igual, mientras que la lemma inferior es 2(3)-nervia y es igual o mayor que el antecio. Asimismo, en *A. ciliatifolius* las láminas son de (5–)12–14(–25) × 0.1–0.2 cm, de ápice acuminado.

10. Axonopus magallanesiae Giraldo-Cañas, Caldasia 22: 23. 2000. TIPO: Venezuela. Bolívar: Distrito Cedeño, meseta de Jaua, sector centro-meridional, cabeceras del río Marajano, afluente del río Cácaro, 1750–1800 m, 20 Nov. 1989, *O. Huber 12995* (holotipo, COL no visto; isotipos, MO-5331971!, MYF no visto, foto ex MO en SI!, SI!, VEN no visto). Figuras 2A–C, 7.

Plantas perennes, densamente cespitosas, de 30–50 cm de altura, con rizomas gruesos y cortos; cañas aplanadas, de 2 mm de diámetro, 2-nodes, delgadas, simples, erguidas, pajizas, longitudinalmente estriadas, con surco lateral conspicuo, glabras; nudos castaño rojizo, vilosos; vainas levemente mayores que los entrenudos, conspicuamente estriadas, pajizas, los bordes hialinos, glabras, con pelos largos hacia el borde, más densamente hacia el cuello, equitantes, de manera que las láminas resultan notablemente dísticas; nervios de las vainas se continúan en la lámina; cuello conspicuo con una región triangular castaño rojizo hacia los márgenes, glabro, con pelos largos hacia el borde, similares a los de la vaina; aurículas y contralígula ausentes; lígulas membranáceo-ciliadas, 0.5 mm; láminas lineares, a veces levemente arqueadas, rígidas, (3–)6–9(–10) × 0.5–0.6 cm, dispuestas en la base y porción mediana de las cañas, plegadas hasta el ápice, obtusas o subagudas, base continua con la vaina, longitudinalmente estriadas en ambas caras, con nervio central y laterales conspicuos, ambas caras glabras, con ápice escabriúsculo plegado, retuso, partido en hojas viejas, rara vez hipofilo con pelos ralos. Cañas floríferas con 1 inflorescencia naciendo del último nudo caulinar, con pedúnculo aplanado, con surco lateral notable, longitudinalmente estriado, glabro; inflorescencia compuesta por 3–5 racimos de 4–8 cm, siendo los basales alternos y los apicales opuestos, raquis ligeramente ondulado, triquetro, de 0.4–0.5 mm de ancho, cara dorsal plana, cara ventral con costilla conspicua, hispídulo, más conspicuamente sobre los ángulos, sin pelos largos o bien con pelos hasta de 1.5 mm de la altura de la inserción de los pedicelos; pedicelos de 0.2–0.5 mm, aplanados, hispídulos, glabros o laxamente pilosos, con 1–5 pelos hialinos hasta de 1.5 mm. Espiguillas de contorno oblongo-elíptico, 2.1–2.3(–2.5) × 0.9–1 mm, dorsiventralmente comprimidas, agudas, ocráceas, alternas, dispuestas laxamente en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a otra de la otra hilera en 0–1/4(–1/3) de su longitud; gluma superior y lemma inferior membranáceo-hialinas, gluma superior de 1.9–2.1(–2.3) mm, menor que el antecio, obtusa, 4–5-nervia, el nervio medio poco prominente o ausente, los restantes conspicuos, submarginales, glabra, lemma inferior de 2–2.1(–2.5) mm, glumiforme, igual al antecio, obtusa, 4–5-nervia, glabra; lemma superior de 2–2.1(–2.5) mm, castaña, poco brillante, glabra, con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente menor que la lemma, glabra. Cariopsis no vista.

Distribución geográfica y ecología. Crece en Venezuela en el T.F. Amazonas, Departamento Atures, en los cerros Yaví y Coro Coro, y en el estado de Bolivar en la meseta Jaua del Parque Nacional Jaua-Sarisariñama. Habita en áreas de bosques ribereños, arbustales y herbazales tepuyanos de los alrededores del río Marajano, en la altiplanicie meridional de la Meseta de Jaua, entre los 1750–2200 m.

Fenología. Coleccionada en flor y/o fruto en los meses de octubre y noviembre.

Axonopus magallanesiae es afín a *A. flabelliformis*, por presentar vainas equitantes y láminas notablemente dísticas; *A. flabelliformis* se distingue por incluir ejemplares de mayor porte, de 0.55–1.20 m de altura, sus láminas de 10–20(–60) cm y sus inflorescencias generalmente con 6–20(–30) racimos, de 5–15 cm, las espiguillas son de menor tamaño, de (1.3–)1.6– (2.2) mm, la gluma superior es 2(–3)-nervia y la lemma inferior es 2-nervia.

El análisis del material tipo permitió observar que la pilosidad de los pedicelos es variable dentro de una misma inflorescencia, hallándose pedicelos glabros y otros pilosos, con 1 a 5 pelos hialinos laxamente distribuidos a lo largo del pedicelo.

Material examinado. VENEZUELA. **Amazonas:** Atures, cumbre del Cerro Coro-Coro, en las cabeceras NW del

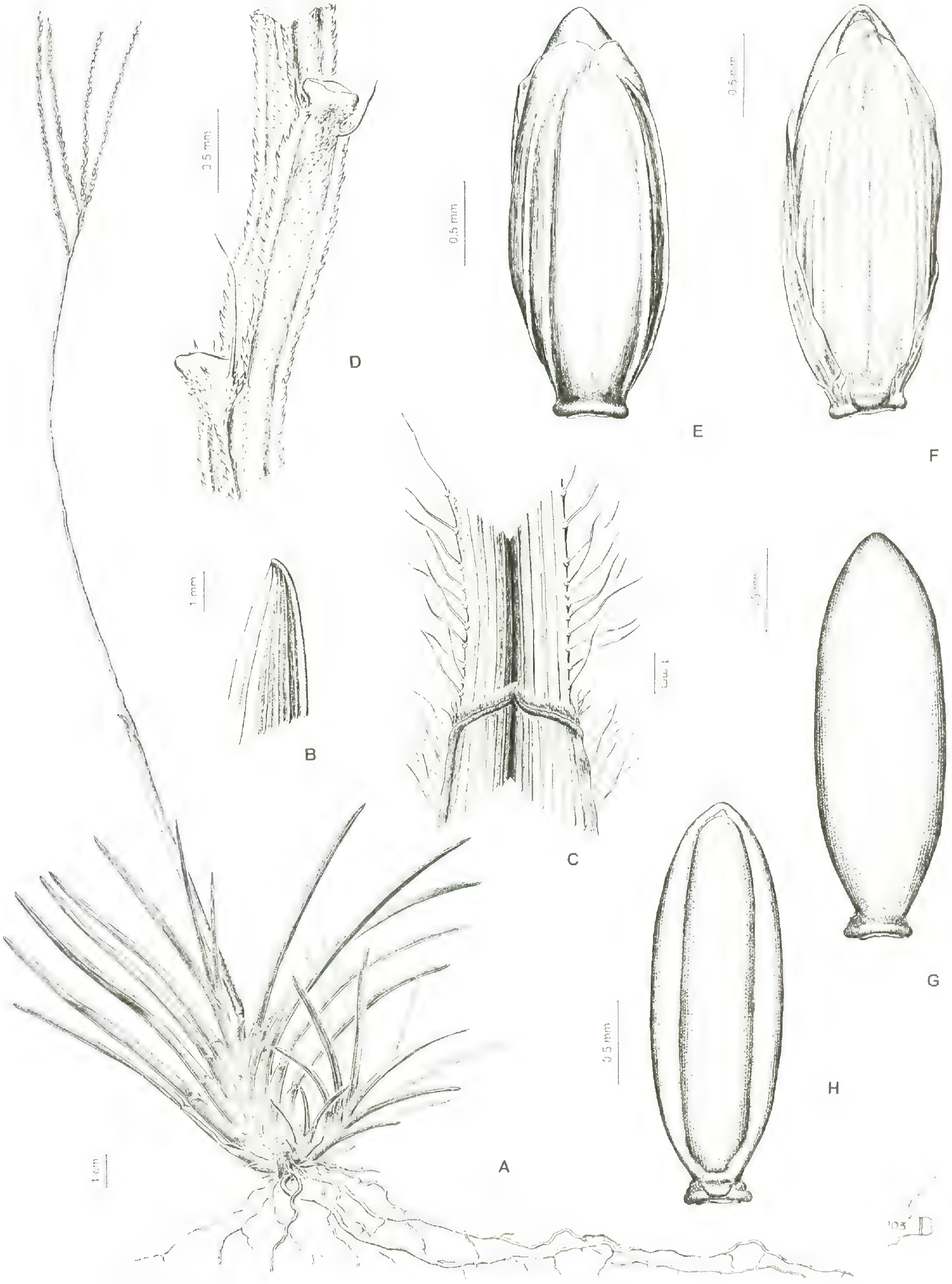

Figura 7. *Axonopus magallanesiae* Giraldo-Cañas (dibujado del isotipo *Huber 12995*, SI). —A. Hábito. —B. Detalle del ápice de una lámina. —C. Detalle de la región ligular. —D. Detalle de una porción del raquis. —E. Espiguilla vista del lado de la gluma superior. —F. Espiguilla vista del lado de la lemma inferior. —G. Antecio superior visto del lado de la lemma. —H. Antecio superior visto del lado de la pálea.

Río Manapiare, *Huber 12339* (SI); Atures, Cumbre del Cerro Yaví, cabeceras del Río Parucito, *Huber 11882* (SI).

11. Axonopus pennellii G. A. Black, Advancing Frontiers Pl. Sci. 5: 142. 1963. TIPO: Colombia. Meta, Villavicencio, sandy open hillside, near Río Guatiquia, 700–900 m, 26–31 Ago. 1917, *F. W. Pennell 1539* (holotipo, US 1041805!; isotipos, foto ex US en SI!, NY!). Figuras 1F, 8.

Plantas perennes de 0.70–1.20 m de altura, cespitosas, con rizomas cortos; cañas generalmente aplanadas, de 3–4 mm de diámetro, con surco lateral notable, 2- ó 3-nodes, simples, longitudinalmente estriadas, glabras, cubiertas por las vainas basales; nudos castaños, levemente engrosados, glabros o con escasos pelitos a vilosos; vainas menores que los entrenudos, longitudinalmente estriadas, pajizas, glabras; nervios de las vainas se continúan en la lámina; cuello imperceptible; contralígula y aurículas ausentes; lígulas membranáceo-ciliadas, 0.3–0.4 mm, castañas, con márgen blanquecino; láminas acintadas anchas, herbáceas, (10–)30–45 × (1–)1.4–1.5 cm, predominantemente basales en la planta, plegadas solamente en la base y planas hacia el ápice, éste conspicuamente acuminado, la base continua con la vaina, longitudinalmente estriadas y escabriúsculas en ambas caras, con nervio central y laterales conspicuos y pelos largos, delgados y dispersos en toda la superficie de ambas caras, el márgen escabriúsculo y viloso en toda su extensión. Cañas floríferas con 1–2 inflorescencias naciendo del último nudo caulinar, pedúnculos ligeramente angulosos, con estrías longitudinales poco conspicuas, glabros; inflorescencia con (12–)18–26 racimos de 9–15 cm; raquis notablemente ondulado a recto, 0.3–0.5 mm de ancho, pajizo en la zona central, verdoso en los márgenes, triquetro, cara dorsal plana, cara ventral con costilla conspicua, hispídulo o escabriúsculo en toda su superficie, más conspicuamente sobre los ángulos, sin pelos largos; pedicelos de 0–0.3 mm, conspicuamente aplanados, hispídulos. Espiguillas de contorno oblongo-elíptico, de 1.6–1.9(–2.1) × 0.6–0.8 mm, dorsiventralmente comprimidas, ocráceas, alternas, dispuestas en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a otra de la otra hilera en 1/3 de su longitud; gluma superior de 1.9–2.1 mm, mayor que el antecio, aguda, 2(–3)-nervia, con pelos largos y delgados, dispersos, más densamente en hilera a ambos lados de los nervios; lemma inferior de 1.8 mm, mayor que el antecio, 2–3-nervia, con igual indumento que la gluma superior; lemma superior de 1.8–1.9 mm, aguda, castaña, glabra, con escasos y cortos pelitos en su ápice, rara vez sin ellos, con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente menor que la lemma, glabra. Cariopsis no vista.

Distribución geográfica y ecología. Hasta el momento ha sido coleccionada en Colombia (Meta) y en Venezuela (Barinas). Crece en lugares abiertos, sobre suelos arenosos a altitudes medias entre los 200–900 m.

Fenología. Coleccionada en flor y/o fruto entre los meses de agosto y noviembre.

Número cromosómico. $n = 10$ (nota en el ejemplar *Davidse 318*, US, VEN).

Anton (1982) menciona que en *Axonopus pennellii* los nudos son pilosos. Sin embargo, en el material tipo de esta especie, los nudos son glabros o con muy escasos pelitos.

Axonopus pennellii se distingue fácilmente por sus hojas anchas de 14–15 mm, con ápice notablemente acuminado. Por el hábito robusto de las plantas y las láminas anchas, *A. pennellii* se acerca a *A. succulentus* y *A. pressus*. *Axonopus succulentus* se aparta por tener aurículas y ápice de las láminas retuso; *A. pressus* por otra parte, se distingue por la presencia de innovaciones comprimidas, pajizas, cubiertas con vainas de disposición dística en la base de la planta. *Axonopus hoehnei* es también afín a *A. pennellii* por presentar láminas foliares largamente acuminadas (véase observaciones bajo *A. hoehnei*).

Material examinado. COLOMBIA. **Meta:** Sierra de la Macarena, N escarpment, *Philipson 2282* (US). VENEZUELA. **Barinas:** 16 km al SW de Mérida intersection just outside of Barinas, *Davidse 3183* (US, VEN).

12. Axonopus polydactylus (Steud.) Dedecca, Bragantia 15: 273. 1956. Basónimo: *Paspalum polydactylum* Steud., Syn. Pl. Glumac. 1: 19. 1853, como "*P. polydactylon*". TIPO: Brasil: Bahia, sin fecha, *P. Salzmann s.n.* (holotipo, P no visto; isotipos, BAA 2257! fragm. ex P, US 2855750! fragm. ex P, US 558295!). Figuras 2D, E, 9.

Plantas perennes, conspicuamente cespitosas, de (0.50–)0.90–1.20 m de altura, rizomatosas, poco robustas; cañas delgadas, gráciles, aplanadas en la base, luego cilíndricas, de 2–3 mm de diámetro, 5- ó 6-nodes, simples, pajizas, longitudinalmente estriadas, con surco lateral poco conspicuo, glabras; nudos castaño rojizo, levemente comprimidos, glabros; vainas menores que los entrenudos, conspicuamente estriadas, pajizas, conspicuamente laciniadas y fibrosas cuando viejas, glabras o con algunos pelos largos en el borde hacia el cuello a vilosas; cuello im-

Figura 8. *Axonopus pennellii* G. A. Black (dibujado del isotipo *Pennell 1539*, NY). —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción del raquis con espiguilla. —D. Espiguilla vista del lado de la lemma inferior. —E. Antecio superior visto del lado de la pálea. —F. Antecio superior visto del lado de la lemma.

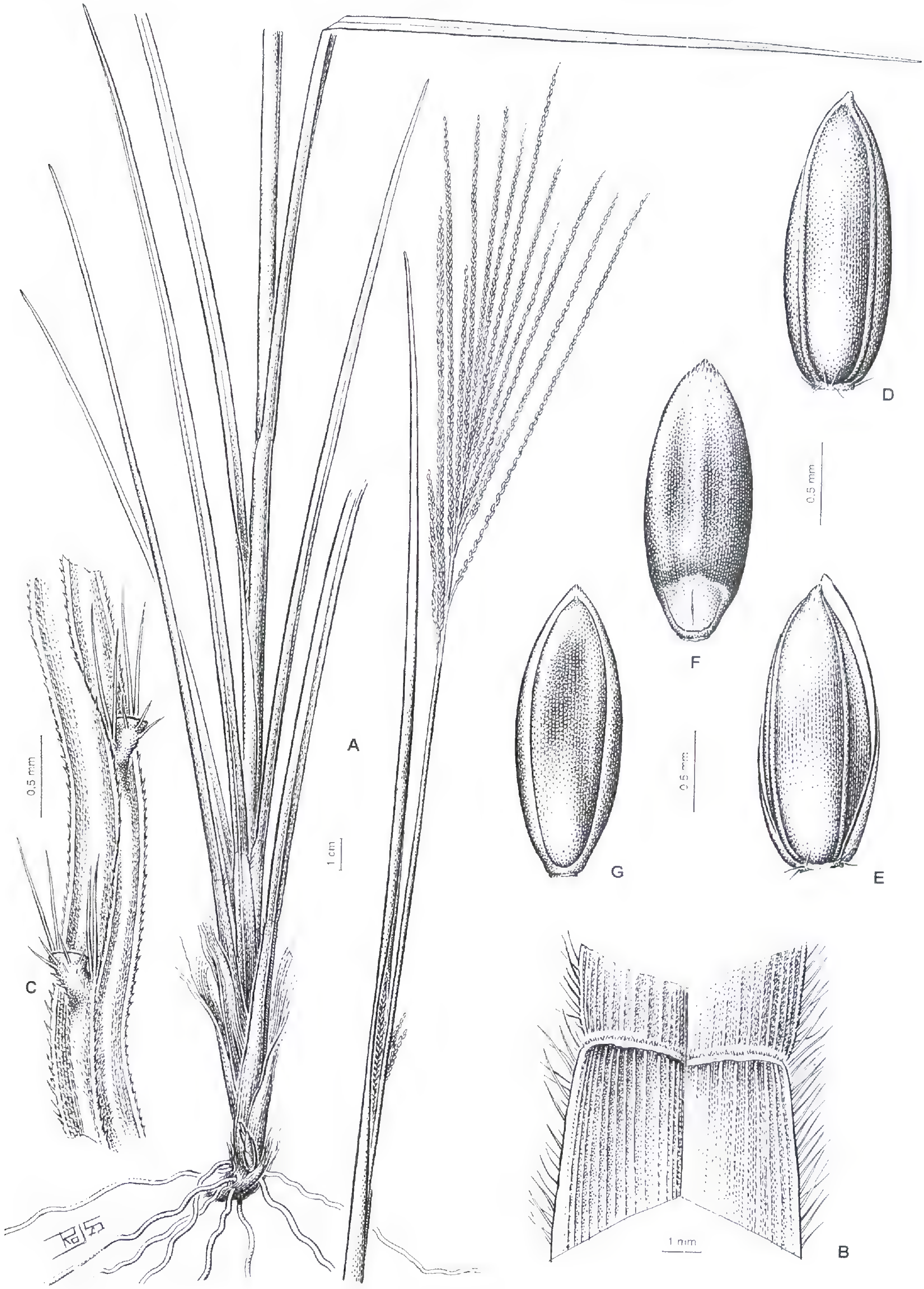

Figura 9. *Axonopus polydactylus* (Steud.) Dedecca (de *Zuloaga et al. 4819*, SI). —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción del raquis. —D. Espiguilla vista del lado de la gluma superior. —E. Espiguilla vista del lado de la lemma inferior. —F. Antecio superior visto del lado de la lemma. —G. Antecio superior visto del lado de la pálea.

perceptible, pajizo, glabro; contralígula y aurículas ausentes; lígula membranácea, de 0.4–0.5 mm, con márgen densamente pestañoso, el resto glabra; nervios de las vainas se continúan en la lámina; láminas lineares, herbáceas, de 20–40(–60) × 0.4–0.6 cm, predominantemente basales en la planta, plegadas en la base, planas hacia el ápice, de ápice agudo, base continua con la vaina, sin pseudopecíolo, longitudinalmente estriadas en ambas caras, con nervio central y laterales conspicuos, glabras o escabriúsculas en el epifilo, de márgen escabriúsculo, o con escasos pelos de 2.5–3 mm cerca de la base, espaciándose hacia el ápice de la lámina o con la cara abaxial vilosa. Cañas floríferas con 1 ó 2 inflorescencias, cada una de ellas con pedúnculo aplanado, glabro, longitudinalmente estriado; inflorescencia con (5–)11–17(–30) racimos mayormente en verticilo, los basales alternos, 7.5–18(–30) cm, cada racimo compuesto por espiguillas alternas, dispuestas en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a otra de la otra hilera en 1/3–2/3 de su longitud; raquis desde apenas ondulado hasta notablemente sinuoso, 0.3–0.4 mm de ancho, triquetro, cara dorsal plana, pajiza en la zona central, verdosa hacia los márgenes, cara ventral con costilla conspicua, a veces pubérulo, hispídulo sobre los ángulos, sin pelos largos, excepcionalmente con escasos (1–4) pelos largos (1.5–2 mm), blanquecinos, más o menos rígidos situados sobre los ángulos a ambos lados de la base de cada pedicelo; pedicelos brevísimos (0.1–0.2 mm), más espaciados en la base del racimo y más cercanos hacia el ápice del mismo, ligeramente aplanados, glabros, a veces pubérulos. Espiguillas dorsiventralmente comprimidas, de contorno oblongo-elíptico, 1.2–1.6(–2) × 0.6–0.9 mm, ocráceas; gluma superior y lemma inferior membranáceo-hialinas, a veces violáceas cerca de los nervios, agudas, glabras u ocasionalmente con algunos pelitos dispersos, gluma superior igual o superando en 0.2 mm el largo del antecio, 2-nervia, lemma inferior igual al antecio, 2-nervia; lemma superior endurecida, subaguda, ca. 1.3 mm, castaña, brillante, glabra, con escasos pelitos cortos en el ápice, con densas y diminutas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y de superficie lisa, encerrando los bordes de la pálea; pálea superior de igual consistencia y aspecto que la lemma superior, ligeramente menor que la lemma, glabra. Cariopsis no vista.

Distribución geográfica y ecología. Endémica del norte y noreste de Brasil (Bahia, Ceará, Goiás, Maranhão, Pará, Minas Gerais, Pernambuco y Rio Grande do Norte). Habita en cerrados y restinga, sobre suelos rocosos o arenosos, entre 0–1200 m, formando densas matas.

Fenología. Encontrada en flor y/o fruto entre los meses de diciembre y abril (junio).

Axonopus polydactylus se caracteriza por su hábito densamente cespitoso, con vainas basales senescentes laciniadas, fibrosas, cañas plurinodes (con 5 ó 6 nudos), láminas angostas (4 a 6 mm de ancho), plegadas, inflorescencias pluriracemosas, con raquis delgado (0.3–0.4 mm de ancho), espiguillas pequeñas (1.2–1.6 mm), distribuidas laxamente a lo largo del raquis y antecio superior en general cortamente escabroso.

Esta especie se halla estrechamente relacionada a *Axonopus suffultus* por sus inflorescencias pluriracemosas, distinguiéndose esta última por tener las vainas basales marcadamente comprimidas, glaucas, no fibrosas, el raquis de las inflorescencias más ancho (0.4–0.7 mm de ancho), las espiguillas mayores (1.8–2.5 mm) y antecio superior glabro. Además, *A. suffultus* crece en sur de Brasil, Paraguay, Uruguay y noreste y centro de Argentina. También es afín a *A. elegantulus* (veáse observaciones bajo esta especie).

En la descripción original de *Paspalum polydactylum* Steudel (1853–1855) menciona que esta especie presenta las glumas 1-nervias a obscuramente 5-nervias. Sin embargo, en el material tipo se ha observado que la gluma superior y lemma inferior son 2-nervias.

Axonopus polydactylus es una especie polimorfa en relación a la pilosidad de las hojas e inflorescencias. Se hallaron ejemplares con laminas vilosas, como en *Swallen 3612*, *Zuloaga et al. 4819* y *4855*, *Chase 3737* y *3775*, y otros glabros como en *Swallen 4034*. Con respecto a la pilosidad del raquis de los racimos, si bien es frecuente que el mismo sea glabro, en algunos ejemplares, como en *Swallen 3612* y *4034*, *Zuloaga et al. 4855*, *Swallen 3737* y *4536* e *Irwin et al. 14656*, se observaron 1–4 pelos hialinos hasta de 2 mm, junto a la inserción de los pedicelos. Tambien se observaron espiguillas con algunos pelitos dispersos sobre la gluma superior y la lemma inferior en *Zuloaga et al. 4855* y *4819*.

Se observaron ejemplares cuyas inflorescencias presentan racimos de 25–30 cm, como en *Swallen 3555*, *3737*, *3750 1/2*, *3761* y *4084*. Asimismo, en los especímenes *Swallen 4028* y *Valls et al. 8332* se encontraron racimos inferiores ramificados, carácter poco frecuente en el género (véase observaciones bajo *Axonopus flabelliformis*).

En el ejemplar *Chase 8003* se encontraron en una misma inflorescencia espiguillas con la gluma superior y lemma inferior 3-nervias y otras 2-nervias.

Axonopus purpurellus y *A. flabelliformis* var. *decipiens* fueron consideradas como sinónimos de *A. polydactylus* (Anton, 1982); en este trabajo, se

consideran en la sinonimia de *A. flabelliformis* (véase observaciónes bajo esta especie).

Material adicional examinado. BRASIL. **Bahia:** Parafuso, 39 km NE of Bahia, *Chase 8003* (NY, US); Mun. Mucugé, de Mucugé a Jussiape, 6 km del desvío de Jussiape, de la ruta a Barra de Estiva, *Zuloaga et al. 4819* (IBGE, MO, SI); Mun. Ilheus, ruta de Olivença a Una, 17 km de Olivença, *Zuloaga 4855* (IBGE, MO, SI); ca. 4 km SW of Belmonte, on road to Itapebí, *Harley et al. 17324* (US). **Ceará:** Campo Grande, *Swallen 4536* (US); Campo Sales to Crato, *Swallen 4327* (US). **Distrito Federal:** Brasília, *Riedel 134* (US). **Goiás:** Rio Piau, ca. 225 km SW of Barreiras on road to Posse, *Irwin et al. 14656* (NY, US); Rio da Prata, ca. 6 km S of Posse, *Irwin et al. 14512* (NY, US); Mun. Tocantinópolis, ribeirao do Corrego, 55 km SW of Estreito along Belém–Brasilia Hwy. (BR 153), *Plowman et al. 9241* (US). **Maranhão:** Grajahú to Porto Franco, *Swallen 3801* (US); Mun. Imperatriz, Belém–Brasília Hwy. (BR 010), 30 km S of Imperatriz, *Plowman et al. 9283, 9291* (US); Carolina to San Antonio de Balsas, *Swallen 4034* (R, US); Barra do Corda to Grajahú, *Swallen 3612* (NY, US), *3754* (BAA, US). **Pará:** Mun. Tucuruí, Breu Branco, km 40 S of represa Tucuruí along Hwy. BR 422, *Plowman et al. 9663* (US); Mun. Marapanim, Campo de Matapiquara, ca. 1 km E of Matipaquara, *Davidse et al. 17900* (US). **Pernambuco:** Tapéra, *Pickel 2547* (US). **Piauí:** Beiras, *Gardner 2365* (US). **Rio Grande do Norte:** Estremoz to Natal, *Swallen 4764, 4765, 4766* (US).

13. Axonopus pressus (Nees ex Steud.) Parodi, Notas Mus. La Plata, Bot. 3(17): 23. 1938. *Paspalum pressum* Nees ex Steud., Syn. Pl. Glumac. 1: 23. 1853. TIPO: Brasil, sin loc., 1836, *F. Sellow 5638* (holotipo, B no visto; isotipos, BAA 2258! fragm. ex B, LE-TRIN-0512.01 fragm. ex B no visto, P!, US 2942557! fragm. ex B). Figura 10.

Axonopus derbyanus G. A. Black, Advancing Frontiers Pl. Sci. 5: 127. 1963. TIPO: Brasil. Mato Grosso: Campo Grande, campo, 540–550 m, 9(7–11) Feb. 1930, *A. Chase 10836* (holotipo, US 1501229!; isotipos, foto ex US en SI!, MO 3326809!, NY 346101 no visto, foto ex NY en SI!, US 1501230!).

Axonopus derbyanus G. A. Black var. *parvispicula* G. A. Black, Advancing Frontiers Pl. Sci. 5: 130. 1963. TIPO: Brasil. Goiás: Goiandira, 800–825 m, 26 Mar. 1930, *A. Chase 11552* (holotipo, US 1448902!; isotipo, foto ex US en SI!).

Plantas perennes, frecuentemente robustas, de 0.7–1.5(–2) m de altura, cespitosas, con rizomas falciformes, 1–2 cm de largo, gruesos, con innovaciones ascendentes, falcadas, originalmente subterráneas y cubiertas por numerosos catáfilos rígidos, pajizos, ligeramente comprimidas y notablemente dísticas; cañas robustas de 3–4 mm de diámetro, leve a marcadamente comprimidas, 2- ó 4-nodes, simples, con surco lateral conspicuo; nudos pajizos a castaño rojizo, comprimidos, glabros; vainas superando los entrenudos en la base, luego menores que los mismos, predominantemente basales, las inferiores fasciculadas, conduplicadas, aquilladas, longitudinalmente estriadas, pajizas, glabras a densamente hirsutas hacia la porción superior o densamente vilosas en toda la superfice, los márgenes densamente pilosos en toda su longitud o solo hacia el ápice de la vaina, excepcionalmente glabros; nervios de las vainas se continúan en la lámina; cuello conspicuo, pajizo a rojizo, glabro a densamente viloso en toda su superficie o bien solo cerca de los bordes; lígulas membranáceo-pestañosas, 0.5–2.5 mm, pajizas, lustrosas, con pelos hasta de 1.5 mm, rara vez el margen muy cortamente ciliado, glabras, a veces la cara abaxial cortamente pubescente; contralígula y aurículas ausentes; láminas acintadas anchas, rígidas, (10–)20–45 × 0.8–1.2 cm, predominantemente basales en la planta, poco divergentes del caule, plegadas en la base, luego planas, con sus bordes frecuentemente revolutos cuando secas, con ápice retuso, cortamente mucronado, frecuentemente hendido a la vejez, la base angosta continuándose imperceptiblemente con la vaina a redondeada, pajizas, longitudinalmente estriadas en el hipofilo, menos conspicuamente en el epifilo, hipofilo glabro con pelos ralos sobre el nervio medio, a densamente viloso en toda la superficie, principalmente hacia los bordes, epifilo glabro a ralamente viloso en los bordes, márgenes escabriúsculos. Cañas floríferas con 1–2 inflorescencias en el último nudo caulinar, cada una de ellas con pedúnculo cilíndrico, longitudinalmente estriado, con surco lateral poco conspicuo, glabro; inflorescencias formadas por (10–)26–34 racimos, excepcionalmente menos, de (10–)13–32 cm, siendo los basales alternos y distantes, los apicales más próximos entre sí; raquis ondulado o recto, pajizo, triquetro, cara dorsal plana, 0.6–0.7(–1) mm de ancho, pajiza en la zona central, verdosa hacia los bordes, cara ventral con costilla conspicua, hispídulo en los ángulos, a veces también hispídulo sobre las caras, sin pelos largos, ocasionalmente con 1–2 pelos de 4–6 mm a cada lado de la base de cada pedicelo; pedicelos de 0.2–0.3 mm, aplanados, escabriúsculos en los ángulos, ocasionalmente con algunos pelos largos similares a los del raquis. Espiguillas oblongo-elipsoides, 2.2–3 × (0.7–)0.9–1 mm, dorsiventralmente comprimidas, agudas, ocráceas o con tintes violáceos, alternas en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a una de la otra hilera en 1/4–1/3 de su longitud; gluma superior y lemma inferior de 2.2–3 mm, en general levemente mayores que el antecio, a veces lemma inferior igual al antecio y gluma superior menor, ambas membranáceo-hialinas, delicadas, glabras a vilosas, más densamente hacia ambos lados de los nervios; gluma superior aguda u obtusa, 2(–3)-nervia; lemma inferior con ápice cortamente acuminado, 2(–3)-nervia; lemma

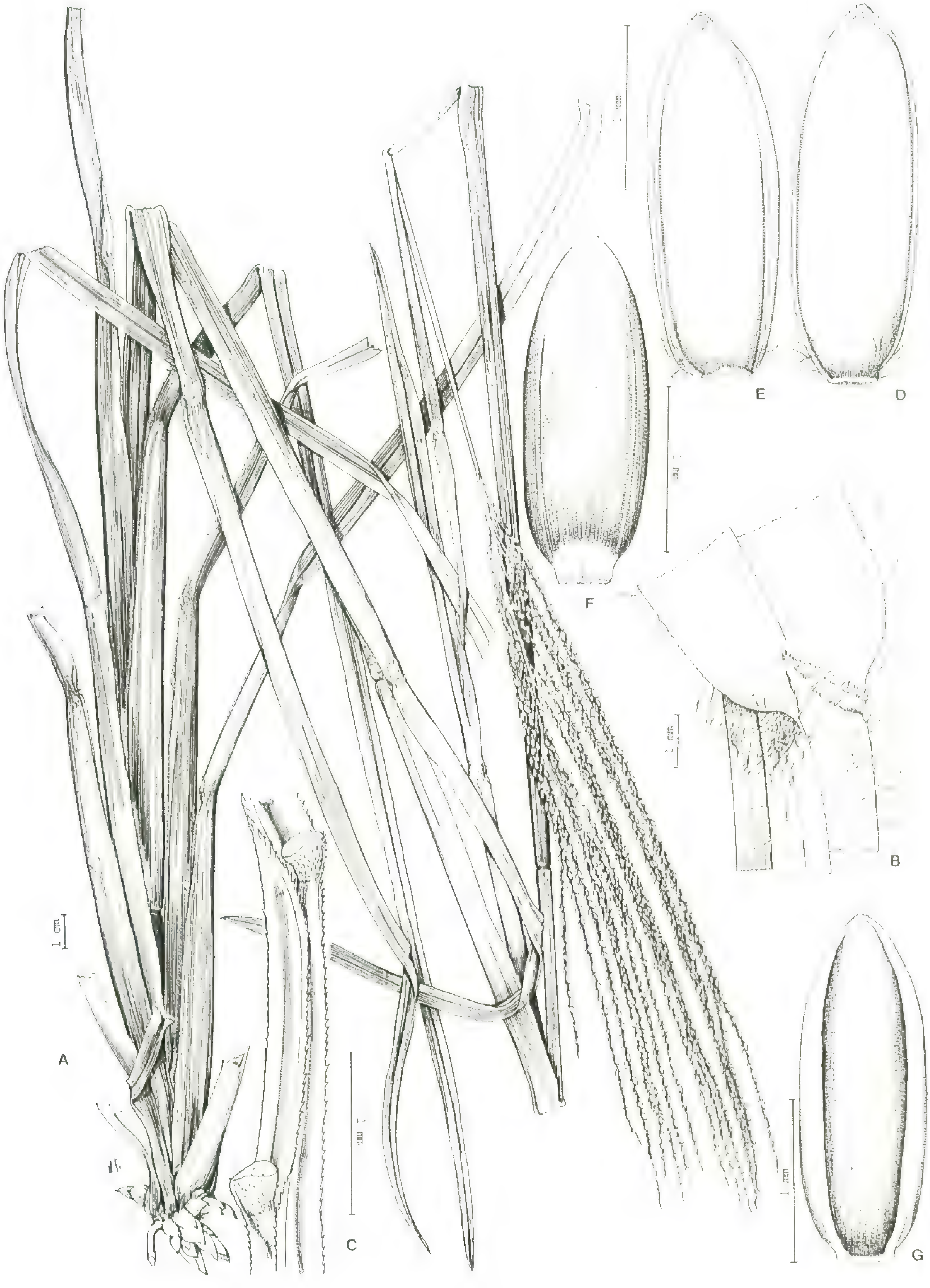

Figura 10. *Axonopus pressus* (Nees ex Steud.) Parodi (de *Solomon et al. 6926*, SI). —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción del raquis. —D. Espiguilla vista del lado de la gluma superior. —E. Espiguilla vista del lado de la lemma inferior. —F. Antecio superior visto del lado de la lemma. —G. Antecio superior visto del lado de la pálea.

superior elipsoide de 2–2.6 × 0.7–1 mm, castaña, brillante, papilosa en toda la superficie, disminuyendo hacia los bordes, glabra o con macropelos y micropelos bicelulares aislados hacia el ápice; pálea superior similar en textura y ornamentación a la lemma, ligeramente menor, glabra; estambres 3, anteras de 1.4–2.5 mm. Cariopsis ovoide, 1.7–1.8 × 0.6–0.8 mm, blanquecino; hilo oblongo, subbasal; embrión 1/2 del largo de la cariopsis.

Distribución geográfica y ecología. Brasil central (Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Rio Grande do Norte y São Paulo), región oriental de Paraguay (Amambay, Caaguazú, Cordillera, San Pedro) y este de Bolivia (Santa Cruz). Crece en cerrados, campos abiertos, en barrancos y en bordes de caminos, sobre suelos arenosos o modificados, entre los 200 y los 1300 m.

Fenología. Coleccionada en flor y/o fruto entre los meses de noviembre y julio.

Nombres vulgares. "Kapi'i misione" (Paraguay, Morrone et al., 1994).

Número cromosómico. n = ca. 20 (Morrone et al., 1995).

La presencia de rizomas falciformes con innovaciones en principio subterráneas y cubiertas por catáfilas pajizas y dísticas es un carácter muy útil para identificar esta especie. *Axonopus pressus* es afín a *A. suffultus*, distinguiéndose esta última especie por el color glauco y violáceo de vainas y láminas, la disposición dística de las vainas, las láminas de mayor tamaño, de 40–55 cm, cuello indistinguible, el raquis de las inflorescencias ralamente a densamente piloso y la ausencia de innovaciones comprimidas lateralmente cubiertas por numerosas vainas. También resulta afín a *A. succulentus*, la que se aparta por la presencia de aurículas foliares. Asimismo, *A. pressus* tiene hojas anchas, similares a las encontradas en *A. flabelliformis* y *A. pennellii*, pero se distingue de ellas porque en éstas el cuello es inconspicuo y glabro y los racimos son más cortos, de 5–15 cm; asimismo, en *A. flabelliformis* la disposición de las vainas basales es dística y en *A. pennellii* las espiguillas son menores, de 1.6–1.9 mm.

Steudel (1853–1855) en su diagnosis original de *Paspalum pressus* señala que la gluma superior y la lemma inferior son 3-nervias. El análisis del material tipo y de ejemplares de herbario permitió observar que la gluma superior y la lemma inferior son 2-nervias, y sólo excepcionalmente se halló en espiguillas aisladas, dentro de una misma inflorescencia, gluma y lemma con nervio medio desarrollado.

En el herbario BAA se estudió un fragmento ex B del isotipo de *Paspalum pressum*, en cuya etiqueta se indica "*F. Sellow 5688*", datos que probablemente se deban a un error de transcripción de la etiqueta original.

Axonopus pressus es una especie polimorfa con una marcada variación en la pilosidad de las vainas, láminas, tamaño y pilosidad de la espiguillas. Steudel (1853–1855), al describir la especie, señala que las vainas son vilosas en los márgenes y las espiguillas son glabras. Black (1963) sigue el mismo criterio en relación a la pilosidad de las espiguillas, pero para las vainas señala que pueden ser escabrosas a densamente vilosas. Sin embargo, entre los ejemplares citados por Black bajo esta especie, algunos presentan espiguillas pilosas, como por ejemplo *Glaziou 16609* y *Chase 11564*. En la misma obra, Black describe *A. derbyanus* y señala su afinidad con *A. pressus*, distinguiéndola por tener espiguillas glabras. El análisis del material tipo y de material de herbario en general permitió determinar que existe una marcada variación en la pilosidad de las vainas, láminas y espiguillas aún dentro de un mismo individuo. Así, el ejemplar tipo *Sellow 5638* presenta espiguillas glabras y otras esparcidamente pilosas; en *Filgueiras & Zuloaga 2097*, *Chase 9092* y *9317* y *Dusén 11686*, las espiguillas son glabras, el raquis presenta pelos en la base de los pedicelos y las vainas son densamente pilosas; otros con espiguillas vilosas, raquis con escasos pelos y vainas densamente pilosas, como en *Clayton 4828* y *Swallen 3733*; con espiguillas, raquis y vainas glabras, es el caso de *Zuloaga & Morrone 4633* y *Morrone & Pensiero 381*; finalmente, ejemplares con espiguillas pilosas, con raquis, vainas y láminas glabras como en *Clayton 4799* y *Rojas 6716*. La variación observada permite incluir *A. derbyanus* en la sinonimia de *A. pressus*.

Black (1963) describe *Axonopus derbyanus* var. *parvispicula* y la distingue por su vainas y láminas densamente vilosas y espiguillas menores de 2–2.2 mm, características que representan parte de la variación presente en la especie, y que justifica la inclusión también en este caso de dicha variedad bajo la sinonimia de *A. pressus*.

Los ejemplares *Krapovickas et al. 14266* y *Morrone & Pensiero 394* se caracterizan por presentar contralígula marcadamente diferenciada, membranácea en la porción basal y ciliada hacia el ápice. Ambos ejemplares han sido coleccionados en la misma localidad, Estancia La Manina, San Pedro (Paraguay), y en el caso del ejemplar *Morrone & Pensiero 394* solamente se hallaron dos plantas con contralígula entre una población de *Axonopus pressus*. Por el momento se incluye a los mismos dentro de esta última especie.

Material adicional examinado. BOLIVIA. **Santa Cruz:** Prov. Velasco, Parq. Nac. Noel Kempff M., serranías S y NE de la pista Noel Kempff M., *Mostacedo et al. 1880* (USZ);

Prov. Velasco, San Ignacio, 2 km hacia SE, *Seidel & Beck 411* (LPB).

BRASIL. **Bahia:** 6 km N of Alagoinhas along Hwy. BR 116, *Davidse et al. 11739* (MO); Mucugé, de Mucugé a Jussiape, 6 km del desvío a Jussiape, de la ruta a Barra da Estiva, *Zuloaga et al. 4816* (IBGE, MO, SI); Espigao Mestre, ca. 100 km WSW of Barreiras, *Anderson et al. 36658* (US). **Distrito Federal:** Brasília, *Clayton 4799, 4828* (US); Rio São Bartolomeu, *Filgueiras & Zuloaga 2120* (IBGE, SI); Barragem da Paranoa, *Filgueiras 2180* (IBGE, SI). **Goiás:** Goiania, *Macedo 4306* (BAA, US); Mun. Niquelândia, Companhia de Niquel Tocantins (CNT), ca. 1 km abaixo da mina de niquel, *Alvarenga et al. 1188* (IBGE, SI); ao longo da rodovia Brasilia–Cristalina, ca. 16 km de Cristalina, *Filgueiras & Zuloaga 2131* (IBGE, SI); Mun. Pirenopolis, Pirineus, *Macedo 1370* (BAA, US); betw. Viannopolis and Posta Funda, *Chase 11330* (US). **Maranhão:** Barra do Corda to Grajahú, *Swallen 3733, 3762* (NY, US); Imperatriz, Bananal, 15 km S of Imperatriz along Belém–Brasilia Hwy. (BR 010), *Plowman et al. 9345* (MO). **Mato Grosso:** close to base camp, ca. 270 km N of Xavantina on the Xavantina–São Felix rd., *Ratter et al. 2078* (US); Mun. Bataguaçu, Corrego Feio, *Hatschbach 23582* (US). **Mato Grosso do Sul:** Campo Grande, *Swallen 9601* (US). **Minas Gerais:** Mun. Arascá, *Macedo 4235* (BAA, US); Serra de Lenheiro, *Glaziou 17428* (BAA, P, US); Serra do Espinhaço, 33 km NE of Francisco Sá, rd. to Salinas, *Irwin et al. 23102* (NY, US); Rod. de Serro a Diamantina, 5 km después del desvío a Pedro Lessa, *Zuloaga & Morrone 4633* (SI); 61 km W of Pará de Minas along Hwy. 262 to Uberaba, *Davidse & Ramamoorthy 10824* (NY). **Pará:** Mun. Conceição do Araguaia, 4 km W of town center along Hwy. PA-150, *Plowman et al. 8988* (US). **Paraná:** Jaguariaiva, Ribeirao 5 Reis, *Hatschbach 9078* (US); Mun. Arapoti, Río das Cinzas, Barra do Perdizes, *Hatschbach 6866* (US). **Rio Grande do Norte:** Entremoz to Natal, *Swallen 4751, 4754, 4759, 4760, 4761* (US). **São Paulo:** Mun. Botucatu, 18 km N of Botucatu, 11 km E of São Manuel, along São Manuel–Piracicaba Hwy., *Gottsberger 979* (US); Mun. Itapetininga, Faz. Santa Luzia do Campo Largo SSE de Itapetininga, *Machado de Campo 189* (BAA, US); São José dos Campos, ca 7.3 km SSE em linha reta da praça, *Mimura 330* (NY, US); Serra da Cunha, *Kuhlmann & Gehrt s.n.* (SI); Mun. Sta. Rita, from Sta. Rita, along road São Simão, *Sendulsky 149* (US).

PARAGUAY. **Amambay:** Sierra de Amambay, Cerro Corá, *Rojas 6872* (BAA, SI); Parq. Nac. Cerro Corá, próxi. al Río Aquidabán, *Morrone & Pensiero 463* (SI); Sierra de Amambay, Cerro Corá, *Rojas 6716, 6716A* (BAA, SI); Parq. Nac. Cerro Corá, *Solomon et al. 6926* (MO, PY, SI). **Caaguazú:** Prope Caaguazú, *Hassler 9269a* (BAA, G); 10 km al N de Caaguazú, camino a Yhú, *López et al. 207* (CTES, SI); Est. Primavera, *Rojas 5112* (BAA, SI). **Cordillera:** Piribebuy, 3 km camino a Paraguarí, *Morrone & Pensiero 114, 394* (SI). **San Pedro:** Ruta 3, 17 km al N de Guayabí, camino a Gral. Isidoro, entrada a la Est. La Manina, *Morrone & Pensiero 381* (SI); 47 km N de San Estanislao, *Krapovickas et al. 14266* (BAA, US).

14. Axonopus ramosus Swallen, Contr. U.S. Natl. Herb. 29: 413. 1950. TIPO: Surinam. Joints in bedrock, Savanna I, Table Mountain (Tafelberg), 565 m, 19 Sep. 1944, *B. Maguire 24816* (holotipo, NY 346107 no visto; isotipos, foto ex NY en SI!, F no visto, U no visto, US 1914998!). Figura 11.

Plantas perennes, gráciles, de 15–80 cm de altura, cespitosas, con rizoma delgado, de entrenudos menores de 0.5 cm, y vástagos muy próximos, paralelos entre sí; cañas delgadas, de 0.5–0.8 mm de diámetro, levemente comprimidas, 4- ó 5-nodes, lisas o con estrías longitudinales casi inconspicuas y surco lateral notable, simples en la porción basal, luego ramificadas, principalmente en la zona media; nudos pajizos a castaños, ligeramente comprimidos, densamente vilosos, con pelos delgados, patentes, blanquecinos, ca. 1 mm, excepcionalmente nudos glabros; vainas menores que los entrenudos, longitudinalmente estriadas, pajizas, con pelos delgados ralamente dispersos sobre toda la superficie, más densamente hacia los bordes y hacia la zona del cuello; nervios de las vainas se continúan en la lámina; cuello conspicuo, pajizo, densamente viloso; contralígula y aurículas ausentes; lígulas membranáceo-ciliadas, 0.2–0.5 mm, blanquecinas, lustrosas; láminas angostamente lineares, rígidas, (3–)10–18(–22) × (0.1–)0.2–0.5 cm, densamente dispuestas en la porción mediana de las cañas, plegadas en la base, luego planas, con ápice conspicuamente agudo, base continua con la vaina, longitudinalmente estriadas en ambas caras, con pelos delgados, de base notablemente tuberculada, ralamente dispersos sobre ambas caras y sobre los márgenes, ocasionalmente láminas glabras. Cañas floríferas con 1–2 inflorescencias naciendo del último nudo caulinar, cada una de ellas con pedúnculo cilíndrico, delgado, glabro, con estrías longitudinales poco conspicuas y surco lateral notable; inflorescencias formadas por 2–4 racimos delgados gráciles, de 3–8 cm; raquis levemente ondulado o recto, triquetro, cara dorsal plana, (0.4–)0.6–0.7(–1) mm de ancho, pajiza en la zona central, verdosa hacia los bordes, hispídulo en toda la superficie, principalmente en los ángulos, sin pelos largos, ocasionalmente con 1–2(–4) pelos a la altura de la base de algún pedicelo; pedicelos de 0.1–0.3(–0.6) mm, aplanados, hispídulos. Espiguillas de contorno oblongo-elíptico, 1.2–1.6 × 0.4–0.7 mm, dorsiventralmente comprimidas, obtusas, ocráceas, alternas en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a una de la otra hilera en 0–1/3 de su longitud; gluma superior igual o menor que el antecio, obtusa, 2–3(4)-nervia, glabra; lemma inferior igual o levemente mayor que el antecio, aguda, 2–3(4)-nervia, glabra; lemma superior elipsoide, 1.1–1.5 mm, castaña, brillante, glabra, con densas y pequeñas papilas en toda la superficie, disminuyendo hacia los bordes, glabra, ocasionalmente con escasos pelitos cortos en el ápice, bordes blanquecinos y lisos, encerrando los bordes de la pálea; pálea superior similar a la lemma, ligera-

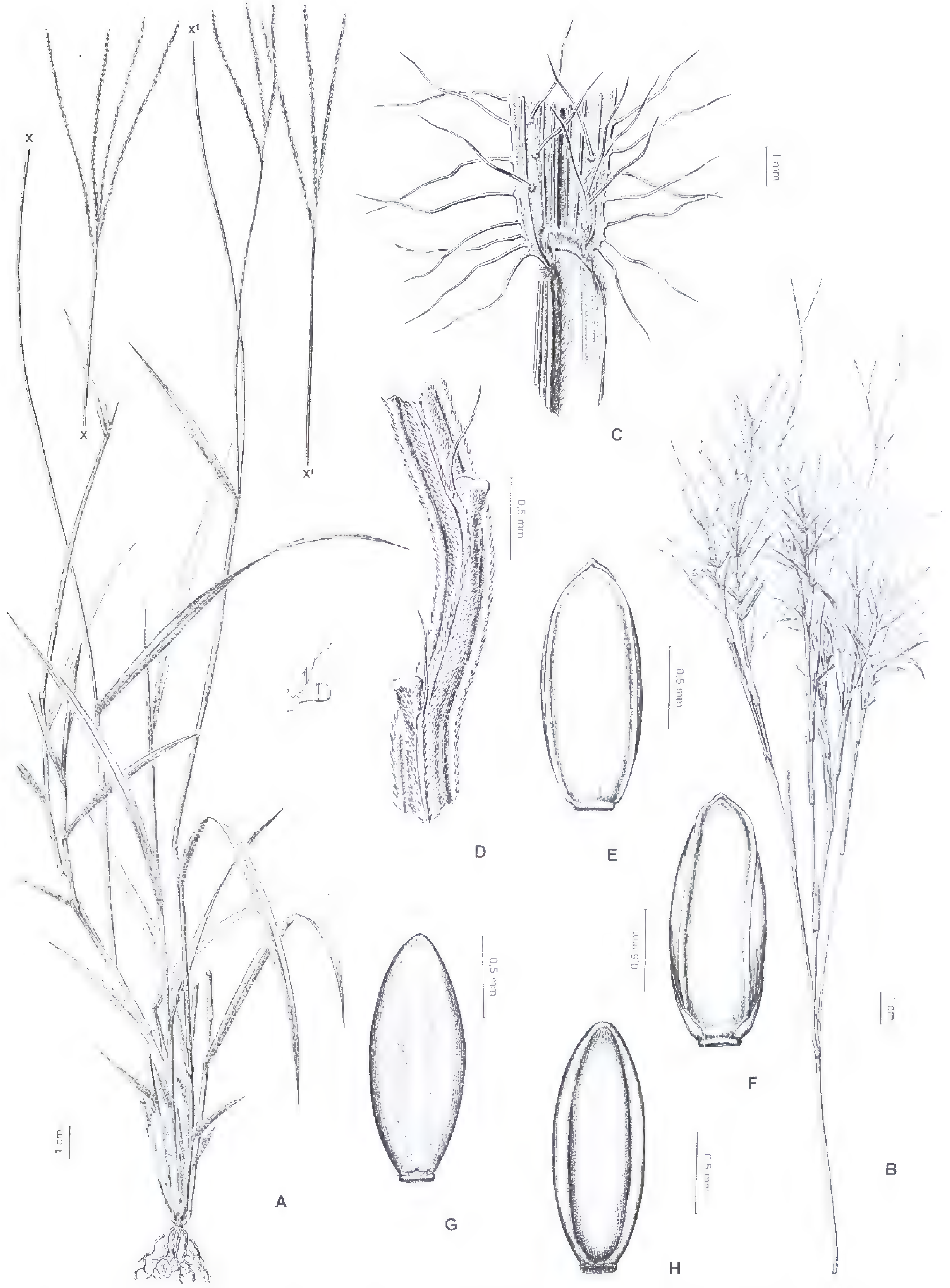

Figura 11. *Axonopus ramosus* Swallen. —A. Hábito. —B. Detalle de una porción de cañas floríferas ramificadas en la región media y superior. —C. Detalle de la región ligular. —D. Detalle de una porción del raquis. —E. Espiguilla vista del lado de la gluma superior. —F. Espiguilla vista del lado de la lemma inferior. —G. Antecio superior visto del lado de la lemma. —H. Antecio superior visto del lado de la pálea. A, C–H, *Maguire et al. 54191* (NY); B, *de Granville 3816* (MO).

mente menor, glabra. Androceo compuesto por 3 estambres con anteras de 0.8 mm. Cariopsis no vista.

Distribución geográfica y ecología. Crece en Surinam, Guayana Francesa y norte de Brasil (Amapá). Habita en zonas montañosas, sobre laderas rocosas, a bajas altitudes desde el nivel del mar hasta los 750 m. Es un elemento predominante en las sabanas.

Fenología. Hallada en flor y/o fruto durante todo el año.

Nombres vulgares. "Kapi'i misione" (Paraguay, Morrone et al., 1994).

Esta especie se distingue por su particular hábito fastigiado, ya que las hojas se concentran en la zona media de las cañas, siendo escasas en la base de las mismas. Las láminas son frecuentemente decíduas y presentan pelos de base conspicuamente tuberculada, ralos sobre la superficie y los márgenes, principalmente en la zona basal de la lámina. Por otra parte, los pelos presentes en las vainas tienen base no tuberculada.

Por su hábito ramificado se asemeja superficialmente a *Axonopus caulescens* (Mez) Henrard, perteneciente a la subserie Scoparii, serie Barbigeri (sensu Black, 1963), pero ésta difiere por el tamaño mayor de las espiguillas, la gluma superior y la lemma inferior 5–7-nervias, con los nervios marcados y el nervio medio usualmente bien desarrollado.

Material examinado. BRASIL. **Amapá:** Inselberg Talouaken, Massif des Tumuc-Humac, *Granville et al. 12239* (MO, US).

GUAYANA FRANCESA. **Haut Oyapock:** Roche Mon Père, *Hook 224* (MO, US); Mont St. Marcel, *de Granville 2631* (MO); Mont Saint-Marcel, zone SE du massif, *Granville et al. 15301* (US); Tumuc Humac, Frontière Brésil-Guyane, *Granville 1230* (US). **Cayenne:** Camp n. 3 Akouba Booka goo Soula, Bassin du Ha Roche 1, *Granville 9860* (US); Haute Canopi, Mont Belvédere, *Hb. Centre Orstom 6969* (MO); Massif des Emerillons, zone centrale Savane roche exposée a l'est sur le flanc coline granitique, *Granville 3816* (MO); Roche Touatou, bassin de L'Oyapock, *Cremers & Granville 13985* (US); Montagne des Nouragues–Bassin de l'Acataye, *Feuillet 4359* (US); Montagne del Nouragues, Bassin de l'Arataye Somnet, *Sarthou 188* (US). **Massif des Emerillon:** zone N savane roche au sommet d'une colline sur la gauche de la Haute Approuagee, *de Granville 3953* (MEXU).

SURINAM. Forested hills 9 km N of Lucie and 12 km W of Oost Riviers, *Mauire et al. 54191* (NY, US); Voltzberg, top II, *Schulz et Donsebar 10597* (US); Lucie Rivier, 2 km NE of island, near affluence of Oost Rivier, *Maguire et al. 54170* (US); Saramacca, Tafelberg, *Kramer et Hekking 2907* (US).

15. Axonopus succulentus G. A. Black, Advancing Frontiers Pl. Sci. 5: 134. 1963. TIPO: Paraguay. Campo serrania, Ybytymí Cordillerita, Feb. 1933, *T. Rojas 6176* (holotipo, US 2012951!; isotipos, foto ex US en SI!, BAA!). Figura 12.

Plantas perennes, robustas, de 0.6–1.2 m de altura, rizomatosas, con vástagos cubiertos por catáfilos rígidos; cañas robustas de 5 mm de diámetro, levemente cilíndricas, 3- ó 4-nodes, simples, longitudinalmente estriadas, glabras; nudos castaños, conspicuos, levemente comprimidos, glabros a pubérulos, principalmente los cercanos a la base de la caña; vainas menores que los entrenudos, longitudinalmente estriadas, pajizas, glabras, bordes lisos, glabros; nervios de las vainas se continúan en la lámina; cuello conspicuo, pajizo, glabro; aurículas presentes; contralígula ausente; lígula membranáceo-ciliada, 1–1.5 mm, pajiza, lustrosa, con cara abaxial pubescente; láminas acintadas, anchas, rígidas, de 30–55 × 1–2 cm, predominantemente basales en la planta, plegadas en la base, luego planas, con ápice retuso, base continua con la vaina, pajizas, longitudinalmente estriadas y glabras en ambas caras, márgenes lisos, rara vez levemente escabriúsculos. Cañas floríferas con 2–3 inflorescencias naciendo del último nudo caulinar, cada una de ellas con pedúnculo cilíndrico, longitudinalmente estriado, con surco lateral conspicuo, glabro; inflorescencias formadas por 15–18(–25) racimos de (8–)12–20 cm, siendo los basales alternos y los apicales más próximos entre sí, verticilados; raquis levemente ondulado, triquetro, 0.4–0.8 mm de ancho, cara dorsal plana, pajizo en la zona central, luego verdoso, cara ventral con costilla conspicua, hispídulo en los ángulos, con 3–4 pelos de 1–1.2 mm a cada lado de la base de cada pedicelo; pedicelos de (0.2–)0.3–0.5 mm, aplanados, glabros o cortamente híspidos. Espiguillas de contorno oblongo-elíptico, 2.1–2.4 × 0.7–1 mm, dorsiventralmente comprimidas, agudas, ocráceas, alternas en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a una de la otra hilera en 0–1/4 de su longitud; gluma superior de 2–2.4 mm, igual o levemente menor que el antecio, aguda u obtusa, 2–3-nervia, con escasos pelitos dispersos, más densos a ambos lados de los nervios laterales; lemma inferior de 2–2.4 mm, igual o ligeramente mayor que el antecio, aguda, 2(3)-nervia, con igual pilosidad que la gluma superior; lemma superior ca. 2–2.2 mm, castaña, brillante, glabra, con densas y pequeñas papilas en toda la superficie, disminuyendo hacia los bordes, glabra, bordes blanquecinos y lisos, encerrando los bordes de la pálea; pálea superior similar a la lemma, ligeramente menor, glabra; estambres 3, anteras ca. 1.5 mm. Cariopsis no vista.

Distribución geográfica y ecología. Especie endémica de la región oriental de Paraguay, en el departamento Paraguarí. Crece en campos.

Fenología. Coleccionada en flor y/o fruto en el mes de febrero.

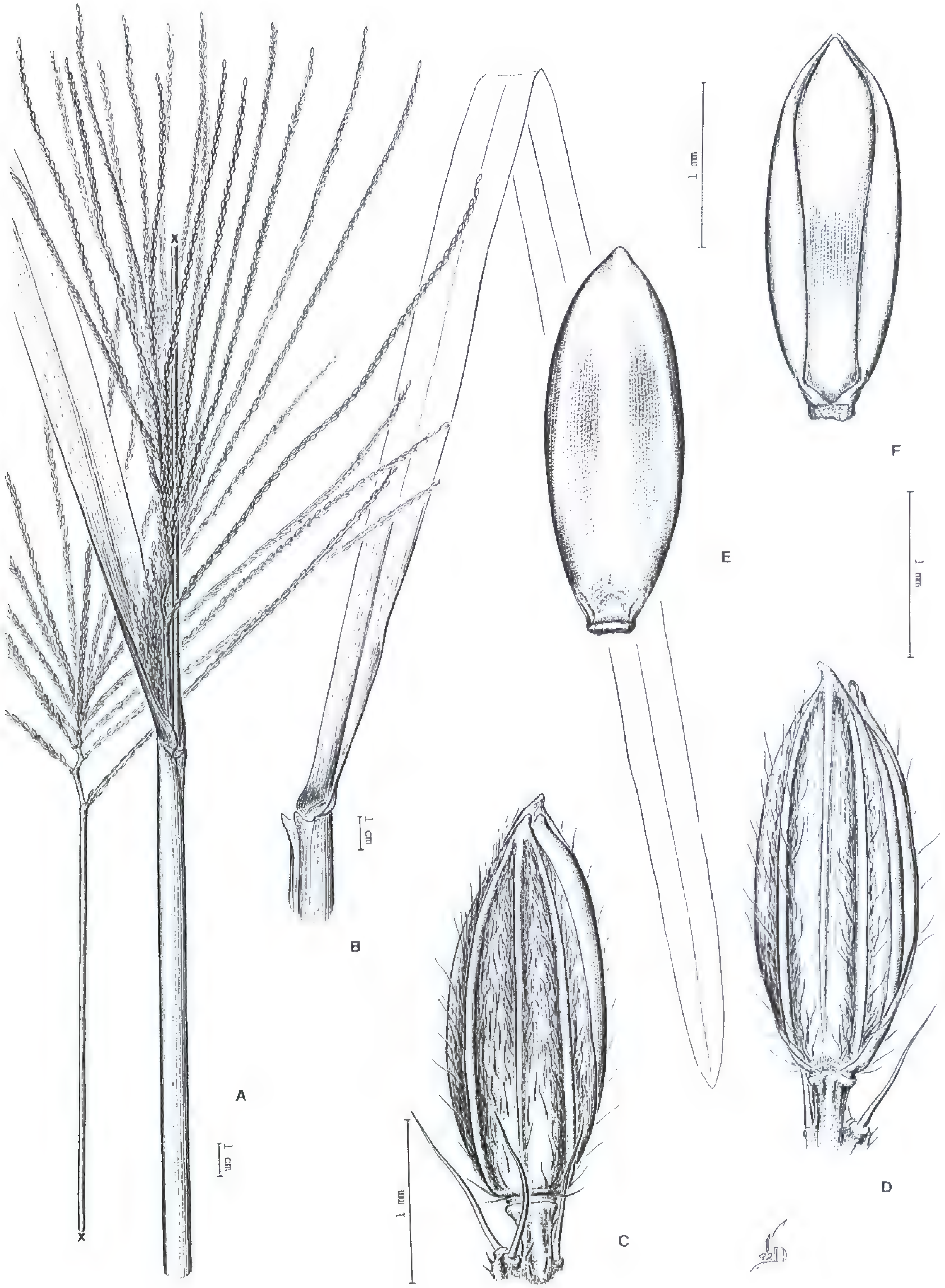

Figura 12. *Axonopus succulentus* G. A. Black (dibujado del holotipo *Rojas 6176*, US). —A. Porción superior de una caña florífera. —B. Detalle de la lámina, con una porción de la vaina. —C. Espiguilla vista del lado de la gluma superior, con pedicelo. —D. Espiguilla vista del lado de la lemma inferior, con pedicelo. —E. Antecio superior visto del lado de la lemma. —F. Antecio superior visto del lado de la pálea.

Nombre vulgar. "Kapi'i kyra" (Paraguay, Morrone et al., 1994).

Esta especie fue considerada por Anton (1982) como sinónimo de *Axonopus pressus*, con la salvedad de que tal vez sea un extremo de la variación de la especie, ya que los pedicelos de las espiguillas son pestañosos. Sin embargo, la presencia de aurículas en la mayoría de las vainas, junto con las hojas más anchas, permite diferenciar ambos taxones.

16. Axonopus suffultus (Mikan ex Trin.) Parodi, Notas Mus. La Plata, Bot. 3(17): 23. 1938. Basónimo: *Paspalum suffultum* Mikan ex Trin., Neue Entdeck. Pflanzenk. 2: 46. 1821. *Panicum suffultus* (Mikan ex Trin.) Kuntze, Revis. Gen. Pl. 3(3): 364. 1898. *Axonopus scoparius* var. *suffultus* (Mikan ex Trin.) Herter, Anales Mus. Hist. Nat. Montevideo, ser. 2, 3(1): 49. 1929. TIPO: Brasil, sin loc., *J. S. Mikan s.n.* (holotipo, LE-TRIN 0537.07 no visto; isotipo, US 80029! fragm. ex LE). Figuras 2F, 13.

Panicum hagenbeckianum Kuntze, Revis. Gen. Pl. 3(2): 361. 1898. *Anthaenantia hagenbeckiana* (Kuntze) Schum., Just's Bot. Jahresber. 261: 329. 1900. *Axonopus hagenbeckianum* (Kuntze) Parodi, Notas Mus. La Plata, Bot. 3(17): 21. 1938. TIPO: Argentina/Bolivia: Gran Chaco, *C. F. Hagenbech s.n.* (holotipo, B no visto; isotipos, BAA 317! fragm. ex B, US 80689! fragm. ex B).

Paspalum iridaceum Mez, Bot. Jahrb. Syst. 56 (Beibl. 125): 10. 1921. *Axonopus iridaceus* (Mez) Hitchc. & Chase ex Rojas, Revista Jard. Bot. Mus. Hist. Nat. Paraguay 2: 160. 1930. *Axonopus hagenbeckianum* (Kuntze) Parodi var. *iridaceus* (Mez) G. A. Black, Advancing Frontiers Pl. Sci. 5: 140. 1963. TIPO: Paraguay: Amambay, Sierra de Amambay, Oct. 1912, *E. Hassler 11113* (holotipo, B no visto; isotipos, BAA 317! fragm. ex B, G!, MO-2101066!, US 725414!, US 2855289! fragm. ex B).

Plantas perennes, de 0.5–1.5 m de altura, densamente cespitosas, con rizomas cortos, y macollos dísticos, de aspecto iridáceo; cañas robustas de 3–6 mm de diámetro, levemente comprimidas, 2- ó 3-nodes, simples, con surco lateral conspicuo, glabras; nervios de las vainas se continúan en la lámina; nudos castaño rojizo a negruzcos, comprimidos, glabros, a veces con algunos pelos largos a la altura del cuello; vainas aquilladas, lateralmente comprimidas, menores que los entrenudos, conspicuamente dísticas, estriadas, generalmente glaucas con zonas violáceas, rara vez pajizas, glabras a vilosas, con bordes lisos, glabros; cuello inconspicuo, pajizo, glabro; lígula membranáceo-ciliada, 0.4–0.5 mm, castaña, contralígula y aurículas ausentes; láminas acintadas, rígidas, de 40–55 × 0.5–1.3 cm, predominantemente basales en la planta, plegadas en la base, aquilladas, luego planas, glaucas a pajizas, con sus bordes frecuentemente revolutos cuando secas, con ápice obtuso, base continua con la vaina, longitudinalmente estriadas en el hipofilo, menos conspicuamente en el epifilo, glabras, a veces con márgenes escabriúsculos. Cañas floríferas con 1–2 inflorescencias naciendo del último nudo caulinar, cada una de ellas con pedúnculo cilíndrico, longitudinalmente estriado, con surco lateral menos conspicuo que en las cañas, glabro; inflorescencias formadas por 12–23(–40) racimos de (6–)11–22 cm, siendo los basales alternos y distantes, los apicales más próximos entre sí; raquis ondulado o recto, triquetro, cara dorsal plana, 0.4–0.7 mm de ancho, con nervio medio notable, purpúreo a blanquecino, cara ventral con costilla conspicua, escabroso en los ángulos, generalmente con (2–)3–4(–6) pelos de 1–2 mm, rígidos sobre los ángulos a cada lado de la base de los pedicelos, rara vez dispersos a lo largo de los ángulos; pedicelos de 0.2–0.5 mm, distantes en la base del racimo, siendo más cercanos hacia el ápice del mismo, notablemente aplanados, escabriúsculos en los ángulos, con algunos pelos largos similares a los del raquis. Espiguillas de contorno oblongo-elíptico, 1.8–2.2(–2.5) × 0.6–1 mm, dorsiventralmente comprimidas, agudas, ocráceas, alternas en 2 hileras sobre el raquis, de tal forma que cada espiguilla se opone a una de la otra hilera en 1/2 de su longitud; gluma superior y lemma inferior iguales o levemente mayores que el antecio, con ápice cortamente acuminado, membranáceo-hialinas, delicadas, con tintes castaños, gluma superior 2(–3)-nervia, lemma inferior 2-nervia, glabra; lemma superior elipsoide, 1.8–2.2(–2.4) mm, castaña, brillante, glabra, con densas y pequeñas papilas en toda la superficie, disminuyendo hacia los bordes, éstos blanquecinos y lisos, encerrando los bordes de la pálea, micropelos bicelulares hacia el ápice; pálea superior similar a la lemma, ligeramente menor, glabra; estambres 3, anteras de 1–1.2 mm, negruzcas. Cariopsis elipsoide, de 1.6 × 0.7 mm; embrión 1/2 del largo de la cariopsis; hilo oblongo.

Distribución geográfica y ecología. Sur de Brasil (Paraná, Rio Grande do Sul, Santa Catarina y São Paulo), Uruguay (Canelones, Cerro Largo, Durazno, Florida, Paysandú, San José y Tacuarembó), Paraguay (Alto Paraná, Amambay, Caaguazú, Cordillera, Guairá, Itapuá, Misiones, Paraguarí y San Pedro) y noreste y centro de la Argentina (Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Misiones y Santa Fe). Crece en suelos bajos, arenoso-arcillosos, húmedos, o bien en suelos pedregosos, secos.

Fenología. Coleccionada en flor y/o en fruto entre los meses de septiembre y abril (julio).

Nombre vulgar. "Palha-dura" (Smith & Wasshausen, 1982).

Figura 13. *Axonopus suffultus* (Mikan ex Trin.) Parodi (de *Rojas 2304*, SI). —A. Hábito. —B. Espiguilla vista del lado de la lemma inferior. —C. Detalle de una porción del raquis, con una espiguilla vista del lado de la gluma superior. —D. Antecio superior visto del lado de la pálea. —E. Antecio superior visto del lado de la lemma. —F. Detalle de la región ligular.

Número cromosómico. $2n = 20$ (Parodi, 1946, sub *Axonopus iridaceus*, Núñez, 1952), $2n = 40$ (de Wet & Anderson, 1956), $n = 10$ (Hunziker et al., 1998).

Según Anton (1982) en el herbario de LE existe una cartulina que lleva varios especímenes correspondientes a dos coleccionistas: tres de ellos coleccionados por *Riedel*, año 1831, Brasil, que corresponden a *Axonopus polydactylus*, y uno coleccionado por *Langsdorff* "in sylvaticis umbrosiis pr. Mandiocam, Brasil" que concuerda con *A. polystachyus*. Este último ejemplar fue citado bajo *Paspalum suffultus* por Trinius (1826: 90), y fue el ejemplar seleccionado para dibujar el hábito de la especie en su obra de 1828 (tab. 108). Los detalles de las espiguillas de la lámina de la obra de Trinius corresponden al ejemplar tipo de *P. suffultus* (*Mikan s.n.*), encontrándose los originales de los detalles pegados en la misma cartulina del ejemplar tipo.

Herter (1956) describe *Axonopus chloridiformis* sobre la base de un ejemplar coleccionado por J. Schroeder. El tipo no pudo localizarse, pero los caracteres dados en la diagnosis original se corresponden con *A. suffultus*.

Axonopus suffultus se caracteriza por su hábito cespitoso, con rizomas de entrenudos cortos, cañas erectas, con las vainas basales marcadamente fasciculadas, éstas usualmente glaucas y violáceas. Se ha observado que ocasionalmente puede presentar estolones de entrenudos largos, que arraigan y dan nuevos macollos, como en el ejemplar *Morrone et al. 1592*. Asimismo, se ha encontrado que ocasionalmente, la gluma superior, la lemma inferior y el raquis son densamente hirsutos. Esta característica se evidencia en el ejemplar *Schwarz 8073*.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Pergamino, Basualdo, *Parodi 6135* (BAA, SI); Pdo. Pergamino, Manuel Ocampo, *Parodi 1912* (BAA). **Chaco:** Dpto. Donovan, 13 km N de la Verde, Est. Dos Tranqueras, *Schinini 22812* (BAA, CTES); Dpto. San Fernando, Fontana, en las orillas del Río Negro, *Meyer 367* (SI). **Córdoba:** Marcos Juárez, *Stuckert 14813* (SI). **Corrientes:** Dpto. Concepción, Est. Tranquera de Hierro, 66 km al NE de Chavarría camino a Concepción, Cerro Puitá, *Arbo et al. 6951* (CTES, LPB); Dpto. Gral. Alvear, Ruta Nac. 14, de Alvear a Santo Tomé, a 12 km de Alvear, *Zuloaga et al. 3102* (SI); Dpto. Ituzaingó, desembocadura del Ayo. Garapé en el río Paraná, *Quarín et al. 2838* (BAA); Dpto. Mburucuyá, Est. Santa Teresa, *Pedersen 1338* (US); Dpto. Mercedes, Colonia Itá Caabó, *Pedersen 6110* (BAA, US); Dpto. San Martín, La Cruz, *Burkart 7938* (SI); Tres Cerros, *Renvoize 2995* (US); Dpto. Santo Tomé, Ayo. Chirimay y Ruta 40, *Tressens et al. 1081* (BAA, CTES); Ruta 41, 5–6 km al N de Galarza, *Ferrucci et al. 6347* (CTES, SI); límite con Misiones, Ayo. Chirimay, *Zuloaga & Morrone 6430* (SI). **Entre Ríos:** Dpto. Federación, Federación, *Burkart 24728* (SI, US); Dpto. Concordia, Concordia, *Parodi 6790* (BAA). **Formosa:** Dpto. Pilcomayo, Laguna Primavera, *Morel 9012* (US); sin departamento, Las Palmas, *Joergensen 2128* (SI). **Misiones:** Dpto. Apóstoles, San José, Escuela Agrotécnica Don Bosco, *Renvoize 3042* (US); Dpto. Candelaria, Santa Ana, *Rodríguez 573* (BAA, SI); Ruta Prov. 3, 10 km del desvío de la Ruta Nac. 12 a Cerro Corá, *Morrone et al. 1751* (SI); Dpto. Capital, Posadas, Est. Santa Inés, *Parodi 1091* (BAA); Dpto. Montecarlo, Pto. Montecarlo, *Porta 102* (BAA, SI); Dpto. San Ignacio, 6 km de San Ignacio, camino al Paraje Payal, *Morrone et al. 1592* (SI); Dpto. San Pedro, San Pedro, *Parodi 5645* (BAA). **Santa Fe:** Dpto. Garay y San Janvier, entre Saladero Cabal y San Javier, *Ragonese 2801* (BAA); Dpto. Gral. Obligado, Mocoví, *Venturi 2381* (BAA); Dpto. San Justo, La Mora, *Ragonese 2712* (BAA). BRASIL. **Paraná:** Ponta Grossa, *Swallen 8320* (US); Serrinha, in campo subpaludoso, *Dusén 17669* (SI, US); Campina Grande do Sul, Estr. Rio Taquary Rio Divisa, *Hatschbach 3568* (BAA). **Rio Grande do Sul:** Caaró, P. S. Luiz, *Rambo 53411* (BAA); Faz. Englert p. S. Fr. De Paula, *Rambo 56320* (BAA); Pelotas, *da Costa Sacco 230* (BAA, US). **Santa Catarina:** Mun. Chapecó, campo, Fazenda Campo São Vicente, 24 km W of Campo Erê, *Smith et al. 9307* (US), *Smith & Klein 13861* (SI, US); Abelardo Luz, 8–12 km N of Abelardo Luz, *Smith & Klein 13338* (SI, US); Bom Retiro, by Fazenda Santo Antonio, Campo dos Padres, *Smith & Reitz 10306* (NY, SI). **São Paulo:** Mun. São Carlos, Porto Pulador on Rio Moji Guacu, 8.9–9 km NNE of the RR station at Sta. Eudoxia, *Eiten & Freitas Campos 3495* (US). PARAGUAY. **Alto Paraná:** Tacurú Pucú, *Fiebrig 6735* (BAA, US); Itaquyry, *Fiebrig 5689* (BAA, G, LIL, SI). **Amambay:** Sierra de Amambay, *Hassler 9729* (G). **Caaguazú:** Palomares, camino de Itaquyry a Curuguaty, *Schinini & Marmori 30059* (CTES, SI); Coronel Oviedo, *Panetti & Rojas 9993* (BAA, SI). **Cordillera:** Camino Caácupé Tobatí, *Rojas 1830* (BAA); Est. Barrerito, Caápucú, campos barranca Riacho Yaguary, *Rojas 11197* (BAA, SI); Itacurubí a San José, km 93, *Burkart 18566* (SI, US). **Guairá:** Plaine de Doña Juana, pres de Villa Rica, *Balansa B. 99* (MO); Santa Bárbara, *Jorgensen 4101* (BAA, LIL, SI); Villarrica, *Rojas 9254* (BAA, LIL, SI); Azucarera Tebicuary, *Rojas 9254a* (BAA, SI, US). **Itapúa:** Isla Yaciretá, *Jiménez 14665, 1465511/2* (SI). **Misiones:** Tebicuary, *Rojas 9254a* (SI); Est. "La Soledad", *Pedersen 4255* (BAA, SI), *Pedersen 7633* (BAA, US). **Paraguarí:** Caápucú, Est. Barrerito, orilla del Ayo. Yaquarí, *Ramírez 430* (BAA, LIL); National Ybicu'i NW corner of park, *Zardini 15970* (MO). **San Pedro:** Villa San Pedro, *Rojas 2304* (SI); Alto Paraguay, Primavera, *Woolston G 77* (SI). **Sin departamento:** Chaco Septentrionalis, *Fiebrig 5374* (G); sud Paraguay, *Kuntze s.n.* (NY). URUGUAY. **Canelones:** ca. del Parq. Racine, *Legrand 991* (BAA). **Cerro Largo:** Río Negro, Est. Palleros, *Gallinal et al. 1235* (BAA, SI). **Durazno:** Est. Las Palmas, *Schrader 18745* (US). **Florida:** Timote, Santa Clara, *Gallinal et al. 3035* (US). **Paysandú:** Meseta de Artigas, Río Uruguay, *Rosengurtt 9283* (BAA, SI, US). **San José:** Barra Santa Lucía, *Rosengurtt 6615* (US). **Tacuarembó:** Gruta de Los Cuervos, 11 km al N de Tacuarembó, *Morrone et al. 5271* (SI). **Sin departamento:** sin loc., *Felippone 5363* (SI).

Especie Excluida de la Serie *Suffulti*

Axonopus mexicanus G. A. Black, Advancing Frontiers Pl. Sci 5: 144, t. 10. 1963. TIPO: México. Sinaloa: ca. 47 mi. E of Villa Unión (1 mi. E of Santa Lucia) on rd. from Villa Unión to Durango, 1280 m, 27 Sep. 1953, *J. R. Reeder & C. G. Reeder 2445* (holotipo, IAN no visto; isotipos, MEXU!, NY no visto, foto ex NY en SI!, SI! fragm. ex MEXU).

Black (1963: 34, 144) incluye *Axonopus mexicanus* dentro de la serie *Suffulti*. Sin embargo, al analizar material del isotipo, se observó que los antecios son pálidos, blanquecinos a pajizos, carácter que no se encuentra presente en especies de la serie *Suffulti*. La presencia de nervio medio marcado, antecio superior pajizo y láminas planas, anchas, permitiría ubicar *A. mexicanus* en la serie Barbigeri (sensu Black, 1963).

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Apéndice 1. Lista de especies aceptadas de la serie *Suffulti* de *Axonopus*.

1. *Axonopus arcuatus* (Mez) G. A. Black
2. *A. argentinus* Parodi
3. *A. ciliatifolius* Swallen
4. *A. cuatrecasasii* G. A. Black
5. *A. elegantulus* (J. Presl) Hitchc.
6. *A. flabelliformis* Swallen
7. *A. gracilis* G. A. Black
8. *A. hoehnei* G. A. Black
9. *A. jeanyae* Davidse
10. *A. magallanesiae* Giraldo-Cañas
11. *A. pennellii* G. A. Black
12. *A. polydactylus* (Steud.) Dedecca
13. *A. pressus* (Nees ex Steud.) Parodi
14. *A. ramosus* Swallen
15. *A. succulentus* G. A. Black
16. *A. suffultus* (Mikan ex Trin.) Parodi

Apéndice 2. Índice de colectores. Cada especimen es ordenado alfabéticamente por su primer colector. El (#) corresponde a la especie (cfr. Appendix 1). Un (*) es utilizado para indicar material tipo.

Alvarenga 1188 (13); *Anderson 9967* (13), *10908* (8), *35179* (13), *36471* (12), *36658* (13); *Araujo 33* (2), *61* (2), *85* (16), *102* (2), *175* (2), *590* (16); *Arbo 1083* (16), *6951* (16); *Archer 4830* (16); *Arechavaleta s.n.* (2); *Asplund 13556* (5).

Baez s.n. (2), *27* (2); *Balansa 97* (2), *99* (16); *Barbosa Cavalcanti 160* (13); *Barreto 1317* (2), *1358* (16), *4689* (16); *Bazzi 14* (16), *401* (16); *Black 46-696* (5); *Boerboom LBB8764* (6); *Buchtien 12* (6); *Burkart 816* (2), *824* (2), *7938* (16), *14350* (16), *18566* (16), *21023* (2), *22922* (2), *22929* (16), *24078* (2), *24728* (16), *25269* (2), *25270* (2), *26192* (16), *26193* (2), *26205* (2).

Cabrera 28146 (16), *28268* (2), *28410* (16), *28728* (16); *Chase 9082 1/2* (13), *9032 1/2* (13), *8914 1/2* (13), *8003* (12), *8820* (13), *8914* (13), *8918* (13), *8922* (13), *9006* (13), *9019* (13), *9032* (13), *9048* (13), *9079* (13), *9082* (13), *9083* (13), *9132* (13), *9133* (13), *9134* (13), *9244* (13), *9317* (13), *9322* (13), *9323* (13), *10487* (13), *11173* (13), *11302* (13), *11330* (13), *11564* (13), *11592* (13), *11603* (13), *11865* (13), *12596* (4); *Clayton 4313* (16), *4799* (13), *4828* (13); *Cowan 1819* (6), *1970* (6); *Cremers 13985* (14); *Cristophal 130* (6); *Cusato s.n.* (16), *1178* (2).

da Costa Sacco 230 (16); *Dauber 111* (2); *Davidse 3183* (11), *4942* (6), *4942* (6), *10824* (13), *10867* (13), *11739* (13), *12079* (13), *17900* (12), *17963* (12), *20751* (1), *22700* (6), *22866* (6); *Davis 40* (6); *de Lemos Fróes 19988* (12), *de Llames s.n.* (2); *Del Mazo s.n.* (2), *8* (2), *25* (2); *Delascio 8324* (6); *Delgado 1108* (6); *Dombrowski 4353* (16); *Dorsett 141 b* (12); *Dusén s.n.* (13), *3934* (13), *11686* (13), *17669* (16); *Dutra 466* (16).

Eiten 2857 (13), *2858* (13), *3771* (12), *3876* (12), *4368* (12); *Eskuche 2528-8* (2); *Essed 34* (6); *Evans 3043* (14).

Felippone 5363 (16); *Ferrucci 6347* (16); *Feuillet 4359* (14); *Fiebrig 5374* (16), *5689* (16), *6735* (16); *Filgueiras 2093* (12), *2097* (13), *2115* (13), *2120* (13), *2134* (13), *2180* (13); *Foldats 314-a* (6); *Fontana F 111-6* (2); *F 180-36* (16), *F 253-4* (16); *Fosberg 27824* (5); * *Friedermann 60* (2).

Galli 54 (2), *287* (2); *Gallinal 1235* (16), *1491* (2), *1199* (2), *1812* (2), *1937* (2), *1947* (2), *2081* (2), *2735* (2), *2907* (2), *3035* (16), *3585* (2), *3991* (2); *Gardner 2365* (12); *Gattoni 13359* (2), *Geyskes 128* (6); *Gillespie 753* (6); *Glaziou 16609* (13), *17428* (13), * *17933* (2), *18672* (13), *22484* (13); *Goodland 906* (6); *Gottsberger 979F* (13); *979* (13), *982* (13), *1011* (13); *Granville 1230* (14), *2631* (14), *3816* (14), *3953* (14), *9860* (14), *12239* (14), *15301* (14); *Gregory 10431* (12).

Hahn 4428 (6); *Harley 11459* (12), *15878* (12), *17075* (12), *17324* (12), *18563* (12); *Harrison 1049* (6); *Hartley 158* (2), *221* (13); *Hassler 9269* (13), *9269a* (13), *9729* (16), *12556* (2), *13031* (2); *Hatschbach 3568* (16), *4178* (16), *6866* (13), *9078* (13), *14010* (13), *14013* (13), *23582* (13); *Henkel 2309* (6); *Henz SJ 35657* (16); *Herb. Centre Orstom 6969* (14); *Hertel 2467* (13); *Hiebert 2* (3), *36* (3); *Hill 27213* (6); *Hitchcock 17285* (6), *22515* (5); *Hoc 158* (16); *Hoehne 28092* (12); *Hoffman 1781* (6), *1945* (6); *Hoock s.n.* (6), *224* (14), *410a* (6), *412* (6), *414a* (6), *420a* (6), *1258* (6), *1265* (6), *1268* (6), *1297d* (6); *Huber 3523* (6), *6217* (6), *7293* (6), *8008* (6), *8174* (6), *9162* (6), *10448* (6), *11882* (10), *12339* (10); *Hutchison 3962* (5).

Irwin BG-83 (6), *12590* (12), *12890* (13), *13340* (13), *14326* (13), *14512* (12), *14656* (12), *19768* (1), *23102* (13), *23506* (13), *27280* (13), *27690* (13), *28812* (13).

Jiménez 140 (13), *14665* (16), *146551/2* (16); *Job 760* (2); *Jorgensen 2428* (16), *4101* (16); *Judziewicz 5410* (6).

Killeen 1577 (4), *1725* (4), *2290* (4); *Kirkbride Jr. 3389* (13); *Klein 3549* (16), *3609* (2), *3657* (16), *3729* (16), *3798* (16); *Kramer 2907* (14); *Krapovickas 12272* (2), *14266* (13), *44594* (16); *Kuhlmann s.n* (13); *39999* (13); *Kunkel 623* (5); *Kuntze s.n.* (16).

Lasser 1500 (6); *Legrand 991* (16); *León 4154* (13); *Lima 194* (13); *Lofgren 3838* (13); *Lombardo 3032* (2); *López 207* (13); *Lourteig 2911* (16); *Luetzelburg 22410* (6), *22954* (6).

Macbride 1498 (5), *3270* (5), *3324* (5), *3760* (5); *Macedo 1734* (13), *3150* (13), *4235* (13), *4306* (13), *4362* (13), *4370* (13), *4534* (13), *4616* (13); *Machado de Campo 188* (13), *189* (13); *Maguire 27* (6), *32477* (6), *32565* (6), *32621* (6), *33719* (6), *54170* (14), *54191* (14); *Martínez Crovetto 3365* (2), *9940* (2); *Mattos 7290* (16), *9841* (12); *Mc Dowell 2972* (6); *Mello Barreto 10637* (13); *Menacho 333* (4); *Mendes Magalhaes 18904* (13); *Meyer s.n.* (16), *32* (2), *67* (16), *89* (16), *367* (16); *Mimura 323* (13), *330* (13); *Miranda 732* (6); *Montes 1304a* (4), *1305a* (4), *12725* (16), *12834* (2), *15230* (16), *15442* (2), *16437* (16), *16442* (2); *Morel 9012* (16); *Morrone* 114 (13), *381* (13), *394* (13), *425a* (13), *432* (13), *463* (13), *720* (2), *1592* (16), *1751* (16), *1767* (16), *1817* (16), *4761* (6), *5271* (16); *Mostacedo 238* (4), *1880* (13); *Múlgura 2170* (16).

Nee 36379 (4), *46906* (3); *Nicora 517* (2), *571* (2), *3071* (2), *5746c* (2).

Núñez 7230 (5).

Oliveira 515 (13); * *Orihuela 60* (2), *63* (2), *300* (2); *Orth s.n.* (16).

Panetti 9993 (16); *Parodi 11* (16), *63* (16), * *91* (2), *157* (2), *1571/2* (2), *4094* (16), *4187* (2), *4326* (16), *4632* (2), * *4649* (2), *4780* (16), *4942* (16), *5645* (16), *6135* (16), *6191* (2), *6294* (2), *6359* (2), *6790* (16), * *9584* (2), *11203* (16), *49432* (16); *Pedelaborde s.n.* (2); *Pedersen 1338* (16), *3638* (2), *4255* (16), *4482* (2), *4712* (2), *5829* (2), *5876* (2), *6110* (16), *6426* (2), *7633* (16); *Pereira 3922* (13); *Peterson 7459* (6); *Philipson 2282* (11); *Pickel 2320* (12), *2547* (12), *5230* (13), *5884* (13), *5886* (13), *5943* (13); *Pinto 1013* (12); *Pires 6156A* (8), *6178* (8), *57983* (13); *Plowman 8988* (13), *9152* (13), *9241* (12), *9283* (12), *9291* (12), *9292* (13), *9345* (13), *9663* (12); *Porta 102* (16); *Pulle 141* (6).

Quarín 1694 (16), *1850* (2), *2838* (16), *2959* (16), *4137* (2).

Ragonese 2712 (16), *2801* (16); * *Rambo 29313* (2), *30763* (16), *35153* (2), *36459* (2), * *36460* (2), *43592* (16), *44003* (16), *44092* (16), *45409* (16), *53411* (16), *53858* (16), *56010* (16), *56320* (16); *Ramírez 407* (16), *430* (16), *649* (2); *Ratter 1038* (13), *2078* (13); *Reitz 2633* (2), *3269* (16), *7798* (16), *11612* (16), *12631* (16), *14147* (2), *17681* (16); *Renvoize 2995* (16), *3042* (16), *3947* (4), *3994* (4), *4029* (4); *Riedel s.n.* (13), *134* (12); *Rodriguez 573* (16); *Rojas 2304* (16), *4830* (16), *5112* (13), *5254* (2), *6704* (2), *6716* (13), *6716a* (13), *6749* (13), *6872* (13), *7964* (16), *9254* (16), *9254a* (16), *13129* (2), *13197* (2), *13202* (2), *13203* (2), *14076* (2), *14105* (2), *14197* (16); * *Rojas 13103a* (2); *Rosa-Mato 1463* (2); *Rosengurtt 305* (2), *B-588* (2), *B-715* (2), *B-825* (2), *B-955* (2), *1063* (2), *B-9189* (16), *B-5391* (2), *B-5335* (16), *6615* (16), *9283* (16); *Rua 38* (2), *123* (13), *138* (16).

Samp 7122 (13); *Sánchez Vega 177* (5); *Sandoval s.n.* (4), *1406* (6); *Sarli 101* (2); *Sarthou 188* (14); *Schinini 14606* (2), *22842* (16), *30059* (16); *Schrader 18745* (16); *Schulz 3269* (2), *3326* (2), *3628* (16), *10597* (14), *11040* (2), *11786* (2), *6310* (16), *6379* (16), *6581* (16), *8073* (16), *8154* (16); *Seidel 411* (13); *Semple 381* (6); *Sendulsky 140* (13), *149* (13), *158* (13), *170* (13); *Simas 35457* (16); *Sin Colector 2503* (6), *8770* (6); *s.n.* (2); *Smith 1000* (6), *8053* (2), *8237* (2), *8629* (2), *9039* (16), *9307* (16), *10306* (16), *13338* (16), *13861* (16), *13990* (2), *15623* (13), *15644* (16), *16039* (2), *13820* (16), *14064* (16), *15473* (16), *12839* (16); *Solomon 6926* (13), *7071* (13); *Soria 5982* (13); *Soukup 1905* (5), *3977* (5); *Steinbach 1979* (4); *Steyermark 59242* (6), *93856* (6), *113164* (6), *127569* (6); *Stuckert 14813* (16); *Swallen 3504* (12), *3612* (12), *3634* (12), *3661* (12), *3696* (12), *3733 bis* (13), *3733* (13), *3734* (12), *3735* (12), *3737* (12), *3738* (12), *3750 1/2* (12), *3753* (12), *3754* (12), *3755* (12), *3757* (13), *3758* (12), *3760* (12), *3761* (12), *3762* (13), *3800* (12), *3801* (12), *3836* (13), *3836 bis* (13), *3986* (12), *3987* (12), *3988* (12), *4028* (12), *4032* (12), *4032 1/2* (12), *4034* (12), *4035* (12), *4035 1/2* (12), *4043* (12), *4048* (12), *4049* (12), *4065* (12), *4084* (12), *4095* (12), *4098* (12), *4142 1/2* (12), *4127* (13), *4142* (12), *4149* (12), *4327* (12), *4536* (12), *4582* (12), *4653* (12), *4749* (13), *4751* (13), *4751 bis* (13), *4754* (13), *4759* (13), *4760* (13), *4760 bis* (13), *4761* (13), *4764* (12), *4765* (12), *4766* (12), *7463* (2), *7544A* (2), *7638* (2), *8110* (2), *8320* (16), *8661* (13), *8662* (13), *8672* (13), *8756* (13), *8968* (13), *8986* (13), *8988* (13), *9023* (13), *9169* (2), *9601* (13), *16940* (6).

Tamayo 4285 (6); *Teunissen 11548* (6); *Tovar 188* (5), *1407* (5); *Tressens 1081* (16), *1457* (16), *1855* (16); *Tutin 621* (6).

Valls 72 (16), *8332* (12), *8364* (12), *8489* (12); *van der Werff 8406* (5); *Vargas 5746* (5); *Venturi 2* (16), *2384* (16).

Whitton 228 (6); *Wiley 475* (3); *Woolston G 73 pro parte* (16), *G 77* (16).

Zardini 11827 (2), *15970* (16), *24075* (16), *24738* (16); *Zuloaga 3102* (16), *4633* (13), *4641* (13), *4737* (13), *4816* (13), *4819* (12), *4855* (12), *6430* (16); *6458* (16), *6551* (16), *6969* (13).

CHROMOSOME REPORTS IN SOUTH AMERICAN NICOTIANEAE (SOLANACEAE), WITH PARTICULAR REFERENCE TO *NIEREMBERGIA*[1,2]

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Abstract

Chromosome counts and karyotype information from 41 populations of 20 species and 6 varieties of Nicotianeae (Solanaceae) from South America belonging to *Bouchetia* Dunal ($x = 8$), *Fabiana* Ruiz & Pav. ($x = 9$), *Leptoglossis* Benth. ($x = 10$), *Nierembergia* Ruiz & Pav. ($x = 8, 9$), and *Petunia* Juss. ($x = 7, 9$) are given, including first reports from 14 taxa: *F. densa* Rémy, *N. ericoides* Miers, and *P. patagonica* (Speg.) Millán, with $2n = 2x = 18$, and *N. browallioides* Griseb., *N. calycina* Hook., *N. graveolens* A. St. Hil., *N. linariifolia* Graham var. *glabriuscula* (Dunal) A. A. Cocucci & Hunz., var. *pampeana* (Millán) A. A. Cocucci & Hunz., and var. *pinifolioides* (Millán) A. A. Cocucci & Hunz., *N. pulchella* Miers var. *pulchella* and var. *macrocalyx* (Millán) A. A. Cocucci & Hunz., *N. rivularis* Miers, *N. tucumanensis* Millán, and *N. reitchii* Hook., with $2n = 2x = 16$. All species studied are diploids, and most have $2n = 16$. In addition, infraspecific polyploidy is recorded for the first time in *N. rigida* Miers ($2n = 4x = 32$) and confirmed in *N. aristata* D. Don ($n = 3x = 24$, $2n = 6x = 48$). In general, karyotypes of the examined species are symmetrical and composed of comparatively small and uniformly sized chromosomes, mostly of the metacentric (*m*) type except in *L. linifolia* (Miers) Griseb., *P. axillaris* (Lam.) Britton, Stern & Poggenb., and *P. patagonica*, where submetacentric (*sm*) chromosomes are predominant. There are one or, rarely, two chromosomes bearing nucleolar organizing regions per basic complement. In *Nierembergia*, karyotype data reflect species grouping. Results suggest that *Bouchetia* is the closest taxon to *Nierembergia*, while *Leptoglossis*, *Petunia*, and *Fabiana* appear more distant. Possible chromosome number evolution in the tribe is speculated based on molecular phylogenetic studies by other authors. In *Nierembergia*, $x = 9$ is proposed to be derived from $x = 8$. Dysploid changes in chromosome number and conservation of chromosome morphology in the karyotypes appear as important evolutionary events in the tribe, while polyploidy is noteworthy only in *Nicotiana* L.

Key words: *Bouchetia*, chromosome numbers, evolution, *Fabiana*, karyotypes, *Leptoglossis*, *Nierembergia*, *Petunia*, polyploidy, Solanaceae, systematics.

The tribe Nicotianeae G. Don (Cestroideae Schltdl., Solanaceae) is composed of plants native to the New World, principally in South America, with *Nicotiana* L. also extending to other continents. As recently proposed by Hunziker (2001), three subtribes are recognized: Nicotianinae Hunz., comprising *Nicotiana* with 67 species (77 after Chase et al., 2003), *Petunia* Juss. with around 34 species (over 40 following Mishiba et al., 2000), and *Fabiana* Ruiz & Pav. (15 species); Nierembergiinae Hunz. & A. A. Cocucci, including *Nierembergia* Ruiz & Pav. (21) and *Bouchetia* Dunal (3); and Leptoglossinae Hunz., encompassing *Leptoglossis* Benth. (7), *Hunzikeria* D'Arcy (3), and *Plowmania* Hunz. & Subils (1, *P. nyctaginoides* (Standl.) Hunz. & Subils). Although much cytogenetic work has been carried out in *Nicotiana* (Goodspeed, 1954; Japan Tobacco, 1994; Chase et al., 2003) and *Petunia* (Wijsman et al., 1983; Maizonnier, 1984; Mishiba et al., 2000), the remaining genera of Nicotianeae have been poorly studied karyologically (see Table 1).

The chromosome number and karyotype information of 20 South American species belonging to five genera of Nicotianeae, i.e., *Bouchetia*, *Fabiana*, *Leptoglossis*, *Petunia*, and *Nierembergia*, are reported herein as a part of a broad cytogenetic study. Our work in *Nierembergia* and related taxa has the following objectives: (1) to report original counts and karyotype analyses for karyologically unknown taxa in Solanaceae, (2) to increase our knowledge of the systematic relationships in the tribe Nicotianeae, and (3) to gain a better insight into chromosomal variation and

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Table 1. Previously published chromosome counts in Nicotianeae (Solanaceae), excluding *Nicotiana* and *Petunia*. Valid names for *Nierembergia* species according to Cocucci & Hunziker (1995). Synonymous names under which chromosome counts were originally published are indicated in brackets.

Taxon	*n*	2*n*	Reference
Hunzikeria texana (Torr.) D'Arcy [sub nom. *Leptoglossis texana* (Torr.) A. Gray]	16		Whalen (1979)
Bouchetia anomala (Miers) Britton & Rusby	8		Di Fulvio (1978)
Bouchetia erecta Dunal	8		Whalen (1979)
Fabiana denudata Miers	9		Moscone (1992)
Fabiana imbricata Ruiz & Pav.	9		Desai (1970)
		18	Goodspeed (1933)
Leptoglossis linifolia (Miers) Griseb.	10		Subils (1979)
Leptoglossis schwenckioides Benth. [sub nom. *Salpiglossis schwenckioides* (Benth.) Wettstein]		20	Diers (1961)
Nierembergia aristata D. Don [sub nom. *N. stricta* Miers]	8		Di Fulvio (1976a)
	24		Di Fulvio (1984)
Nierembergia linariifolia Graham var. *linariifolia* [sub nom. *N. hippomanica* Miers]	8		Di Fulvio (1976a)
	9		Ratera (1952)
		16	Di Fulvio (1976a)
Nierembergia repens Ruiz & Pav.		16	Shizukawa & Mii (1997)
Nierembergia rigida Miers [sub nom. *N. aristata* Sweet]	8		Di Fulvio (1978)
	9		Ratera (1969)
Nierembergia scoparia Sendtn. [sub nom. *N. frutescens* Durieu]		18	Goodspeed (1933)

possible karyo-evolutionary trends, especially in the subtribe Nierembergiinae.

Bouchetia is a small genus of hemi-cryptophytes displaying a disjunct distribution, with *B. anomala* (Miers) Britton & Rusby in southern Brazil, Paraguay, Uruguay and north to central Argentina, and two other species in North America (Hunziker, 2001). On the other hand, *Fabiana* is a western South American endemic taxon of microphyllous and resiniferous shrubs or chamaephytes distributed along the Andes from southern Peru to southern Chile and Argentina, which reaches lowland regions in Patagonia. Considering the shrubby species examined here, *F. densa* Rémy inhabits southern Bolivia and northwestern Argentina, *F. denudata* Miers extends from northern Chile through northern and central Andean areas of Argentina reaching northern Patagonia, and *F. imbricata* Ruiz & Pav. grows in the central and southern Andean regions of Argentina and Chile (Barboza & Hunziker, 1993).

Leptoglossis comprises xerophytic species inhabiting Peru except for the one examined here, the perennial herb *L. linifolia* (Miers) Griseb., endemic to the central and western Argentine lowlands (Hunziker & Subils, 1979). *Petunia* is a South American genus, with one species also in Central and North America. Concerning the two entities here analyzed, *P. axillaris* (Lam.) Britton, Stern & Poggenb. is an annual herb growing in southern Brazil, Bolivia, Uruguay, and Argentina and *P. patagonica* (Speg.) Millán is a chamaephyte endemic to the Argentine province of Santa Cruz (Figueroa Romero, 1999; Hunziker, 2001).

Finally, *Nierembergia*, focused on in this contribution, is South American (except for one species in Mexico), with its principal distribution in the western and southern regions, and the center of diversification in Argentina where 15 species are found (Hunziker, 2001). Its members have nectarless flowers and, in most cases, are unique in the family for producing oils that attract oil-collecting bees (Cocucci, 1991). Several species have become noteworthy as poisonous weeds toxic to cattle, valuable ornamentals, useful plants for genetic engineering, or for potential pharmacological uses with respect to cardenolides and their antitumoral activity (Gil et al., 1995; Godo et al., 1997; Hunziker, 2001).

Species presently studied include all life forms known in *Nierembergia*; they grow in distinct habitats and may have either a widespread or restricted geographical distribution. Some are small shrubs that grow mainly in mountain regions, i.e., *N. browallioides* Griseb., *N. ericoides* Miers, *N. linariifolia* Graham var. *glabriuscula* (Dunal) A. A. Cocucci & Hunz. and var. *pinifolioides* (Millán) A. A. Cocucci & Hunz., *N. pulchella* Miers, and *N. tucumanensis* Millán, or in lowlands, i.e., *N. graveolens* A. St.-Hil., *N. linariifolia* var. *linariifolia* and var. *pampeana* (Millán) A. A. Cocucci & Hunz., and *N. scoparia* Sendtn. Others are rhizomatous, stoloniferous, or tuber-bearing, prostrate (rarely ascendent) herbs from meadows and marshes,

i.e., *N. aristata* D. Don, *N. calycina* Hook., *N. repens* Ruiz & Pav., *N. rigida* Miers, *N. rivularis* Miers, and *N. veitchii* Hook. *Nierembergia rigida* and *N. linariifolia* exhibit the broadest geographical distribution, extending from southern Brazil to southern Argentina, reaching Patagonia, while *N. tucumanensis*, *N. veitchii*, *N. browallioides*, and *N. pulchella* are mainly distributed in northwestern Argentina, the last two species also found in southern Bolivia. *Nierembergia aristata*, *N. graveolens*, *N. scoparia*, and *N. rivularis* inhabit southern Brazil, Uruguay, and northeastern Argentina, with the first species reaching Paraguay and the last one into Bolivia. Lastly, *N. calycina*, *N. ericoides*, and *N. repens* are endemic to eastern Argentina and Uruguay, Argentina (Buenos Aires province), and southern Chile, respectively (Millán, 1941; Cosa de Gastiazoro, 1989; Cocucci & Hunziker, 1995).

Materials and Methods

The provenance of plant material studied is presented in Table 2. The respective voucher specimens were deposited in the herbarium of Museo Botánico de Córdoba, Argentina (CORD).

Somatic chromosomes were observed in squashed root meristems obtained from seed germination. The root apices were fixed in 1:3 acetic acid/ethanol mixture for 12 hours (h) after a pretreatment either in paradichlorobenzene-saturated solution for 2 h at room temperature or in 2 mM 8-hydroxyquinoline for 8 h at 8°C. In most cases, root tips were then stained according to Feulgen's technique by using Schiff's reagent for 1 ½ h in darkness, after hydrolysis in 5 N hydrochloric acid for 50 min at room temperature (Jong, 1997). In some cases, meristems were stained with alcoholic hydrochloric acid-carmine (Snow, 1963) for 3–4 days at room temperature. Meristem cells were isolated, macerated, and squashed in a drop of 2% aceto-carmine after the first procedure or 45% acetic acid after the second staining method. Comparisons of metaphase chromosome size on test preparations after the different pretreatment and staining conditions demonstrated no significant differences between the procedures. Meiotic chromosomes were examined in pollen mother cells from squashed young anthers fixed as described for root apices and stained with aceto-carmine. After staining, slides were made permanent by freezing with liquid CO_2 (Bowen, 1956), removing the coverslip and mounting in Euparal (Chroma, Germany), or without removing the coverslip (Bradley, 1948) and mounting in Rhenohistol (Merck, Darmstadt).

Somatic and meiotic chromosomes were observed and photographed with a Leica DMLB microscope equipped with a Leica DC 250 digital camera and the Leica IM 1000 image management system. Chromosome numbers were determined from 14 to 177 cells of one to 65 seedlings of each species and variety; all counts were made from somatic metaphases, except for the accession *Acosta et al. 32* (CORD), which was analyzed in meiosis (Table 2). Somatic chromosomes were measured and classified according to their arm ratio (r = long arm/short arm length) as recognized after Levan et al. (1964) with the modifications introduced by Schlarbaum and Tsuchiya (1984) as: *m*—metacentric (r = 1.00–1.29), *msm*—meta-submetacentric (r = 1.30–1.69), *sm*—submetacentric (r = 1.70–2.99), *st*—subtelocentric (r = 3.00–6.99), and *t*—telocentric (r = 7.00 and higher).

Leaf and calyx measurements were made from voucher specimens of *N. aristata* and *N. rigida* (Table 3). The Mann-Whitney U-test to at least the 0.01 significance level was used to test for significant differences in the median values between vouchers of the same species with different ploidy level (Sokal & Rohlf, 1995). Statistical analysis was performed by using INFOSTAT, version 1.1 (Infostat Group, 2002).

Results

Chromosome counts from 41 populations of 20 South American species of Nicotianeae (Solanaceae) belonging to *Bouchetia* (1 species), *Fabiana* (3), *Leptoglossis* (1), *Petunia* (2), and *Nierembergia* (13 species, 6 varieties) are reported (Table 2). The somatic chromosome number $2n = 2x = 20$ is found in *Leptoglossis linifolia* (Fig. 1A), while two other figures are observed in *Petunia*, $2n = 2x = 14$ in *P. axillaris* (Fig. 1B) and $2n = 2x = 18$ in *P. patagonica* (Fig. 1C). In addition, $2n = 2x = 18$ is also present in the examined species of *Fabiana*, i.e., *F. densa* (Fig. 1D), *F. denudata* (Fig. 1E), and *F. imbricata* (Fig. 1F), and in two species of *Nierembergia*, *N. ericoides* (Fig. 1H) and *N. scoparia* (Fig. 1I). On the other hand, $2n = 2x = 16$ is recorded in *Bouchetia anomala* (Fig. 1L) and the remaining species of *Nierembergia* studied, i.e., *N. aristata*, *N. browallioides* (Fig. 1G), *N. calycina* (Fig. 2A), *N. graveolens* (Fig. 2D), *N. linariifolia* (Fig. 2E), *N. pulchella* (Fig. 2 B–C), *N. repens* (Fig. 2F), *N. rivularis* (Fig. 2G), *N. rigida*, *N. tucumanensis* (Fig. 2H), and *N. veitchii* (Fig. 2I). In addition, two populations of *N. aristata* display $2n = 6x = 48$ (Fig. 1K), and one sample of *N. rigida* exhibits $2n = 4x = 32$ (Fig. 1J).

The chromosomes are small, ranging from 1.52 to 3.52 μm. The average chromosome length (standard deviation) is 2.54 (0.27) μm in *Bouchetia anomala* and 2.33 (0.24) μm in *Leptoglossis linifolia*, and, in genera where more than one species were examined, it

ranges from 2.30 (0.26)–2.90 (0.38) µm in *Fabiana*, 2.87 (0.30)–3.01 (0.21) µm in *Petunia* (the higher value in *P. patagonica*), and 2.17 (0.23)–2.87 (0.30) µm in *Nierembergia*. Species of the latter genus can be separated into two groups according to chromosome size. On the one hand, *N. browallioides*, *N. linariifolia*, *N. pulchella*, and *N. tucumanensis* all have larger chromosomes, with mean chromosome length values above 2.70 µm. On the other hand, the remaining species display smaller chromosomes, with mean estimates below 2.40 µm, except for *N. calycina* (2.59 µm) and *N. ericoides* (2.61 µm).

Species studied have one chromosome pair carrying nucleolar organizing regions (NORs) plus attached satellites of variable size (e.g., Fig. 1B–E, G–H), except *Bouchetia anomala* (Fig. 1L), *Nierembergia graveolens* (Fig. 2D), *N. linariifolia* var. *glabriuscula*, *N. repens*, and the accession *Di Fulvio 847* (CORD) of *N. aristata*, where two of such pairs were observed. In the examined sample of *L. linifolia* no NORs could be detected (Fig. 1A). Usually, NORs are visible in both members of the respective chromosome pairs, although in several metaphases of each sample they were missing in one homologue (Figs. 1F, I, K; 2F). NORs appear on short arms, except in *N. calycina*, where they were seen on long arms (Fig. 2A).

In general, the Nicotianeae studied have karyotypes with chromosomes that are homogeneous in size and predominantly of the *m* type. The respective karyotype formulae are given in Table 2. Particularly, in *Nierembergia*, *N. browallioides*, *N. calycina*, *N. tucumanensis*, and the varieties of *N. pulchella* (2) and *N. linariifolia* (4) examined, only *m* chromosomes or a majority of *m* and one to two *msm* chromosomes were observed. In contrast, *N. graveolens*, *N. repens*, *N. rigida*, *N. rivularis*, and *N. veitchii* possessed *sm* (1–2) in addition to *msm* (1–2) pairs, while *N. aristata* showed three *msm* pairs. *Leptoglossis linifolia* (7 *sm* pairs), *P. axillaris* (3 *sm* and 1 *msm* pairs), and *P. patagonica* (4 and 1), are distinct in having a minority of *m* chromosomes. *Bouchetia anomala*, the three *Fabiana* species, *N. ericoides*, and *N. scoparia* were the only taxa observed with one *st* pair (in addition to 1 *sm* and/or 1 *msm* pairs), which, in the last two species, was the smallest pair at half the length of the largest pair of the chromosomal complement (Fig. 1H–I).

Statistical comparison of leaf and calyx size yields significant differences between $2n = 2x = 16$ and $2n = 6x = 48$ accessions of *Nierembergia aristata* and between $2n = 2x = 16$ and $2n = 4x = 32$ accessions of *N. rigida*, except for the calyx length in the first species, with polyploids exhibiting greater dimensions for these structures than diploids (Table 3). In *N. aristata*, all individuals examined of the accession *Acosta et al. 32* ($2n = 6x = 48$) showed multivalents in diakinesis-metaphase I, with the following configurations being the most frequent: 2 VI + 1 IV + 16 II (27% of the cells) and 2 VI + 18 II (13%) (data not shown).

Discussion

Chromosome counts from 41 populations of 20 species and 6 varieties of Nicotianeae from South America belonging to *Bouchetia*, *Fabiana*, *Leptoglossis*, *Nierembergia*, and *Petunia* are given, including first reports from 14 taxa—*Fabiana densa*, *Nierembergia browallioides*, *N. calycina*, *N. ericoides*, *N. graveolens*, three out of the four varieties of *N. linariifolia* (vars. *glabriuscula*, *pampeana*, and *pinifolioides*), two out of the three varieties of *N. pulchella* (vars. *pulchella* and *macrocalyx* (Millán) A. A. Cocucci & Hunz.), *N. rivularis*, *N. tucumanensis*, *N. veitchii*, and *Petunia patagonica*—and a new chromosome number from *N. rigida* (see Table 2).

Chromosome figures obtained in *Bouchetia anomala*, *Fabiana denudata*, *F. imbricata*, *Leptoglossis linifolia*, *Nierembergia aristata*, *N. repens*, and *N. scoparia* agree with previously published reports, most of these made during meiosis (see Table 1). Furthermore, our findings of $2n = 16$ in five populations of *N. linariifolia* var. *linariifolia* and one of *N. rigida* are in accordance with previous counts by Di Fulvio (1976a, 1978) and suggest that $n = 9$, as cited for both species by Ratera (1952, 1969), is unlikely. Finally, the chromosome number observed in *Petunia axillaris* matches previous records both in meiotic (Ferguson, 1924; Ratera, 1952; Moscone, 1992; Stehmann et al., 1997) and mitotic divisions (Steere, 1932; Sullivan, 1947; Rangaswamy & Shivanna, 1967; Sink & Power, 1978; Watanabe et al., 1996; Badr et al., 1997).

Basic chromosome numbers

Results confirm the basic chromosome numbers already known for the examined genera, i.e., *Bouchetia* ($x = 8$), *Fabiana* ($x = 9$), *Leptoglossis* ($x = 10$), *Nierembergia* ($x = 8, 9$), and *Petunia* ($x = 7, 9$) (Hunziker, 2001). According to the available chromosome information, Nicotianeae exhibits a dysploid series from $x = 7$ to 12 and some other derived basic numbers, which as arranged in decreasing frequency are: $x = 12, 9, 8, 7, 10, 23, 19,$ and 11 (Moscone, 1992; Stehmann et al., 1997; Mishiba et al., 2000; Hunziker, 2001; Chase et al., 2003). All of these numbers are present in *Nicotiana*, where $x = 12$ is the most frequent, as it is the basic number of subgenera *Rustica* (G. Don) Goodsp. and *Tabacum* (G. Don) Goodsp., as well as of seven of the nine sections of

Table 2. List of the taxa and samples studied (all accessions from Argentina unless indicated otherwise), provenance, voucher number (all voucher specimens deposited at CORD), number of seedlings and somatic metaphases (diakinesis-metaphases I in *Acosta et al.* 32) analyzed per sample, somatic chromosome number and karyotype formula. Abbreviations of collectors' name: MCA = M. C. Acosta, JAA = J. A. Ambrosetti, GEB = G. E. Barboza, AC = A. Cicarelli, AAC = A. A. Cocucci, CC = C. Costa, AD = A. Dafni, EDF = E. Di Fulvio, LAD = L. A. Díaz, FE = F. Ehrendorfer, LG = L. Galetto, ATH = A. T. Hunziker, CAK = C. A. Kirkwood, YK = Y. Kurakami, MMe = M. Medina, MMo = M. Moré, EAM = E. A. Moscone, JN = J. Nattero, SS = S. Schneckenburger, ANS = A. N. Sérsic, RS = R. Subils, MT = M. Tomoya, SV = S. Vogel. [ˆ] In parentheses is indicated the number of individuals and metaphases utilized for chromosome measurements per species and variety. *m*, metacentric; *msm*, meta-submetacentric; *sm*, submetacentric; *st*, subtelocentric chromosome. [+] Haploid count in meiosis (diakinesis-metaphase I). * First chromosome report; ** New chromosome number.

Taxon	Provenance and voucher number	No. of seedlings and somatic metaphases analyzed per sample	$2n$	Karyotype formula[ˆ]
Bouchetia anomala (Miers) Britton & Rusby	Prov. Córdoba, Dept. San Justo, betw. Villa Concepción del Tío & Frontera Sur, *EDF 833*.	1, 3	16	6 *m* + 1 *sm* + 1 *st* (5, 6)
B. anomala	Prov. Córdoba, Dept. San Justo, Marull, *EDF 840*.	30, 64	16	6 *m* + 1 *sm* + 1 *st*
B. anomala	Prov. Córdoba, Dept. Punilla, El Durazno, *AAC, ANS & EAM 941*.	34, 110	16	6 *m* + 1 *sm* + 1 st
Fabiana densa Rémy*	Prov. Tucumán, Dept. Tafí del Valle, El Molle, *ATH, GEB & EAM 24884*.	12, 28	18	7 *m* + 1 *sm* + 1 *st* (3, 6)
Fabiana denudata Miers	Prov. Mendoza, Dept. Malargüe, Sierra de Palauco, *JAA, AC & EAM 1417*.	12, 39	18	7 *m* + 1 *sm* + 1 *st* (5, 10)
Fabiana imbricata Ruiz & Pav.	Prov. Chubut, Dept. Futaleufú, Mt. El Dedal, *AAC & SS 404*.	4, 18	18	7 *m* + 1 *sm* + 1 *st* (1, 5)
Leptoglossis linifolia (Miers) Griseb.	Prov. Santiago del Estero, Dept. Ojo de Agua, betw. Loreto & Villa Ojo de Agua, *AAC & ANS 1112*.	12, 33	20	3 *m* + 7 *sm* (3, 5)
Nierembergia aristata D. Don	Prov. Córdoba, Dept. San Justo, betw. Villa Concepción del Tío & Frontera Sur, *EDF 847*.	11, 61	16	5 *m* + 3 *msm* (4, 10)
N. aristata	Prov. Santa Fe, Dept. Capital, betw. La Guardia & Colastiné Norte, *RS, AAC & GEB 1215*.	22, 33	48	?
N. aristata	Prov. Córdoba, Dept. Punilla, San Roque, *MCA, LAD & CAK 32*[+].	2, 5[+]	48	?
Nierembergia browallioides Griseb.*	Prov. Tucumán, Dept. Tafí del Valle, betw. La Bolsa & El Infiernillo, *LG, AAC, ANS & SV 159*.	25, 81	16	6 *m* + 2 *msm* (6, 10)
Nierembergia calycina Hook.*	URUGUAY. Dept. Paysandú, Paysandú, *AAC & ANS 1095*.	8, 43	16	6 *m* + 2 *msm* (3, 5)
Nierembergia ericoides Miers*	Prov. Buenos Aires, Dist. Tandil, Tandil, *AAC & ANS 923*.	9, 21	18	7 *m* + 1 *msm* + 1 *st* (4, 6)
*N. ericoides**	URUGUAY. Dept. Maldonado, Pan de Azúcar, *AAC 1104*.	3, 5	18	7 *m* + 1 *msm* + 1 *st*
*N. ericoides**	URUGUAY. Dept. Lavalleja, Sierras de Solís, *AAC 1106*.	2, 4	18	7 *m* + 1 *msm* + 1 *st*
*N. ericoides**	Prov. Buenos Aires, Dist. Tandil, Tandil, *AAC & ANS 1330*.	10, 31	18	7 *m* + 1 *msm* + 1 *st*
Nierembergia graveolens A. St.-Hil.*	Prov. Entre Ríos, Dept. Federación, Chajarí, *AAC, ANS, MMo, JN & AD 3021*.	1, 14	16	6 *m* + 1 *msm* + 1 *sm* (1, 5)
Nierembergia linariifolia Graham var. *linariifolia*	Prov. Córdoba, Dept. Río Primero, betw. Río Primero & Santa Rosa de Río Primero, *EDF 842*.	37, 85	16	6 *m* + 2 *msm* (8, 10)
N. linariifolia var. *linariifolia*	Prov. Córdoba, Dept. Punilla, Santa María de Punilla, *EAM 162*.	7, 10	16	6 *m* + 2 *msm*

Table 2. Continued.

Taxon	Provenance and voucher number	No. of seedlings and somatic metaphases analyzed per sample	2*n*	Karyotype formula^
N. linariifolia var. *linariifolia*	Prov. Córdoba, Dept. Capital, El Infiernillo, *AAC, ANS & EAM 944.*	1, 3	16	6 *m* + 2 *msm*
N. linariifolia var. *linariifolia*	Prov. Tucumán, Dept. Tafí Viejo, betw. La Sala & Raco, *AAC & ANS 1114.*	1, 4	16	6 *m* + 2 *msm*
N. linariifolia var. *linariifolia*	Prov. Santiago del Estero, Dept. Ojo de Agua, betw. Loreto & Villa Ojo de Agua, *AAC & ANS 1205.*	4, 24	16	6 *m* + 2 *msm*
N. linariifolia var. *glabriuscula* (Dunal) A. A. Cocucci & Hunz.*	Prov. Córdoba, Dept. Punilla, La Posta, *AAC, ANS, FE & EAM 1010.*	2, 5	16	7 *m* + 1 *msm* (3, 6)
N. linariifolia var. *glabriuscula**	Prov. Córdoba, Dept. Punilla, Dos Puertas, *LAD 4.*	9, 39	16	7 *m* + 1 *msm*
N. linariifolia var. *pampeana* (Millán) A. A. Cocucci & Hunz.*	Prov. Río Negro, Dept. Pichi Mahuida, Río Colorado, *AAC & ANS 1265.*	5, 20	16	7 *m* + 1 *msm* (3, 5)
N. linariifolia var. *pinifolioides* (Millán) A. A. Cocucci & Hunz.*	Prov. Córdoba, Dept. Ischilín, betw. Dean Funes & Sauce Punco, *AAC & LAD 1200.*	2, 4	16	6 *m* + 2 *msm* (5, 10)
N. linariifolia var. *pinifolioides**	Prov. Córdoba, Dept. Ischilín, betw. Dean Funes & Tulumba, *AAC & ANS 1318.*	3, 7	16	6 *m* + 2 *msm*
N. linariifolia var. *pinifolioides**	Prov. Córdoba, Dept. Ischilín, Dean Funes, *MCA & LAD 13.*	2, 3	16	6 *m* + 2 *msm*
N. linariifolia var. *pinifolioides**	Prov. Córdoba, Dept. Punilla, La Toma, *AAC 1455.*	6, 43	16	6 *m* + 2 *msm*
N. linariifolia var. *pinifolioides**	Prov. Córdoba, Dept. Punilla, betw. Capilla del Monte & Ongamira, *AAC 1456.*	1, 3	16	6 *m* + 2 *msm*
Nierembergia pulchella Miers var. *pulchella**	Prov. Mendoza, Dept. Las Heras, Villavicencio, *AAC, ANS & CC 1122.*	8, 91	16	7 *m* + 1 *msm* (4, 6)
Nierembergia pulchella var. *macrocalyx* (Millán) A. A. Cocucci & Hunz.*	Prov. La Rioja, Dept. Famatina, Mt. Famatina, *AAC & ANS 972*, leg. MMe.	7, 36	16	8 *m* (4, 6)
Nierembergia repens Ruiz & Pav.	CHILE. Region VIII, Prov. Concepción, betw. Lota & Concepción, *AAC & ANS 961.*	10, 31	16	6 *m* + 1 *msm* + 1 *sm* (4, 5)
Nierembergia rigida Miers	Prov. Córdoba, Dept. San Justo, Marull, *EDF 834.*	29, 53	16	5 *m* + 1 *msm* + 2 *sm* (2, 6)
N. rigida	Prov. Córdoba, Dept. Punilla, Santa María de Punilla, *AAC, ANS & EAM 943***.	8, 58	32	?
Nierembergia rivularis Miers*	URUGUAY. Dept. Soriano, Villa Soriano, *AAC & ANS 1099.*	1, 19	16	5 *m* + 1 *msm* + 2 *sm* (1, 5)
Nierembergia scoparia Sendtn.	URUGUAY. Dept. Paysandú, Tres Bocas, *AAC & ANS 1097.*	6, 36	18	6 *m* + 1 *msm* + 1 *sm* + 1 *st* (3, 5)
Nierembergia tucumanensis Millán*	Prov. Tucumán, Dept. Tafí del Valle, betw. El Infiernillo & Amaichá del Valle, *AAC, YK & MT 1451.*	4, 17	16	7 *m* + 1 *msm* (3, 7)
Nierembergia veitchii Hook.*	Prov. Tucumán, Dept. Tafí Viejo, San Javier, *AAC & ANS 1113.*	7, 24	16	5 *m* + 2 *msm* + 1 *sm* (3, 5)
Petunia axillaris (Lam.) Britton, Stern & Poggenb.	Prov. Córdoba, Dept. Calamuchita, Falda del Sauce, *EAM 189.*	6, 32	14	3 *m* + 1 *msm* + 3 *sm* (3, 6)
Petunia patagonica (Speg.) Millán*	Prov. Santa Cruz, Dept. Lago Argentino, Estancia La Victoria, *AAC & ANS 471.*	26, 125	18	4 *m* + 1 *msm* + 4 *sm* (5, 6)

Table 3. Comparison of leaf and calyx size between populations of different ploidy level in *Nierembergia aristata* and *N. rigida*. All measurements in mm. Range, mean (standard deviation), median, and sample size (n) are given for each variable. ** Median values differ significantly between vouchers of the same species with different ploidy level (p minor to 0.01). Voucher specimens of accessions: *N. aristata* 2x, *Di Fulvio 847*, and 6x, *Subils et al. 4215*; *N. rigida* 2x, *Di Fulvio 834*, and 4x, *Cocucci et al. 943*.

		Leaf size		Calyx size	
Species	Ploidy level	Length	Width	Length	Calyx lobe width
Nierembergia aristata	2x	9.00–30.00 16.32 (5.90) 14.50** n = 50	0.50–2.00 1.24 (0.36) 1.20** n = 50	8.00–15.00 11.33 (2.12) 12.00 n.s. n = 21	0.50–1.20 0.78 (0.18) 0.70** n = 21
N. aristata	6x	11.50–34.00 21.83 (4.91) 21.45** n = 50	1.20–4.50 2.49 (0.91) 2.10** n = 50	10.00–16.00 12.32 (1.48) 12.00 n.s. n = 25	0.70–1.80 1.10 (0.25) 1.00** n = 25
Nierembergia rigida	2x	6.00–24.00 14.95 (4.28) 15.00** n = 50	0.50–0.90 0.59 (0.10) 0.60** n = 50	7.00–22.00 13.24 (3.79) 13.00** n = 25	0.60–1.50 0.90 (0.25) 0.80** n = 25
N. rigida	4x	8.00–37.00 18.67 (7.28) 18.25** n = 50	0.50–1.20 0.75 (0.19) 0.75** n = 50	12.50–23.50 15.98 (2.97) 15.00** n = 25	0.70–2.00 1.25 (0.29) 1.20** n = 25

subgenus *Petunioides* (G. Don) Goodsp.; however, $x = 12$ is absent in the remaining genera of the tribe. In fact, $x = 12$ is by far the most common basic number in the whole family where it is recorded in more than 50% of the species karyologically examined. Although typical in subfamily Solanoideae, this figure is rare in subfamily Cestroideae, with the exception of *Nicotiana*, as it has been cited just in one species of *Schwenckia* L. and in the monotypic *Streptosolen* Miers.

Both $x = 9$ and $x = 8$ appear in four out of the eight genera of Nicotianeae; thus, they are the basic chromosome numbers most widely distributed in the tribe. The former number is found in *Nicotiana* sect. *Alatae* Goodsp. (five of nine species) and section *Suaveolentes* Goodsp. (two species), *Fabiana*, *Nierembergia* (two species), and *Petunia*. In the latter genus, $x = 9$ is the most common number, which appears in those species transferred to *Calibrachoa* La Llave & Lex. by Wijsman (1990) and some of *Petunia* sensu Jussieu (1803). On the other hand, $x = 8$ is the only basic number reported for *Bouchetia* and *Hunzikeria*, the typical number of *Nierembergia*, and one of the numbers of *Nicotiana* sect. *Suaveolentes*, where the complete series is present. With respect to $x = 7$, this is documented in all species of *Petunia* sensu Wijsman (1990) and a few species of *Nicotiana* sect. *Suaveolentes*. Finally, $x = 10$ appears only in *Leptoglossis*, several species of *Nicotiana* sect. *Suaveolentes*, and two of section *Alatae*. It should be noted that the basic chromosome numbers found by us, with the exception of $x = 7$, are also cited in other tribes within subfamily Cestroideae, i.e., $x = 8$ in Cestreae G. Don (*Cestrum* L. and *Vestia* Willd.), $x = 9$ in Latueae Hunz. & Barboza (*Latua pubiflora* (Griseb.) Baill.), and $x = 10$ in Browallieae Hunz. (*Browallia* L.) and Schwenckieae Hunz. (*Schwenckia americana* L.) (Hunziker, 2001; Chiarini, 2003).

For evolutionary considerations, a comprehensive scheme of possible chromosome number changes during speciation in the Solanaceae is still lacking, and even its original basic number is a matter to be clarified. In this sense, Raven (1975) has speculated that $x = 7$ could be the original number for Solanales, while $x = 12$ may have derived from the tetraploid level ($n = 14$) by aneuploid reduction in the early history of Solanaceae, subsequently giving rise to the lower numbers of the series in Nicotianeae by the same mechanism, ending in $x = 7$. Nevertheless, chloroplast DNA sequence analyses support the ancestral placement of Cestroideae sensu D'Arcy (1991) in the family and the apomorphic condition of $x = 12$ (Olmstead & Palmer, 1992; Olmstead et al., 1999).

In the phylogenetic trees presented by Olmstead & Palmer (1992) and Olmstead et al. (1999), where a broad sample of Solanaceae genera was included, one may speculate a hypothetical direction of

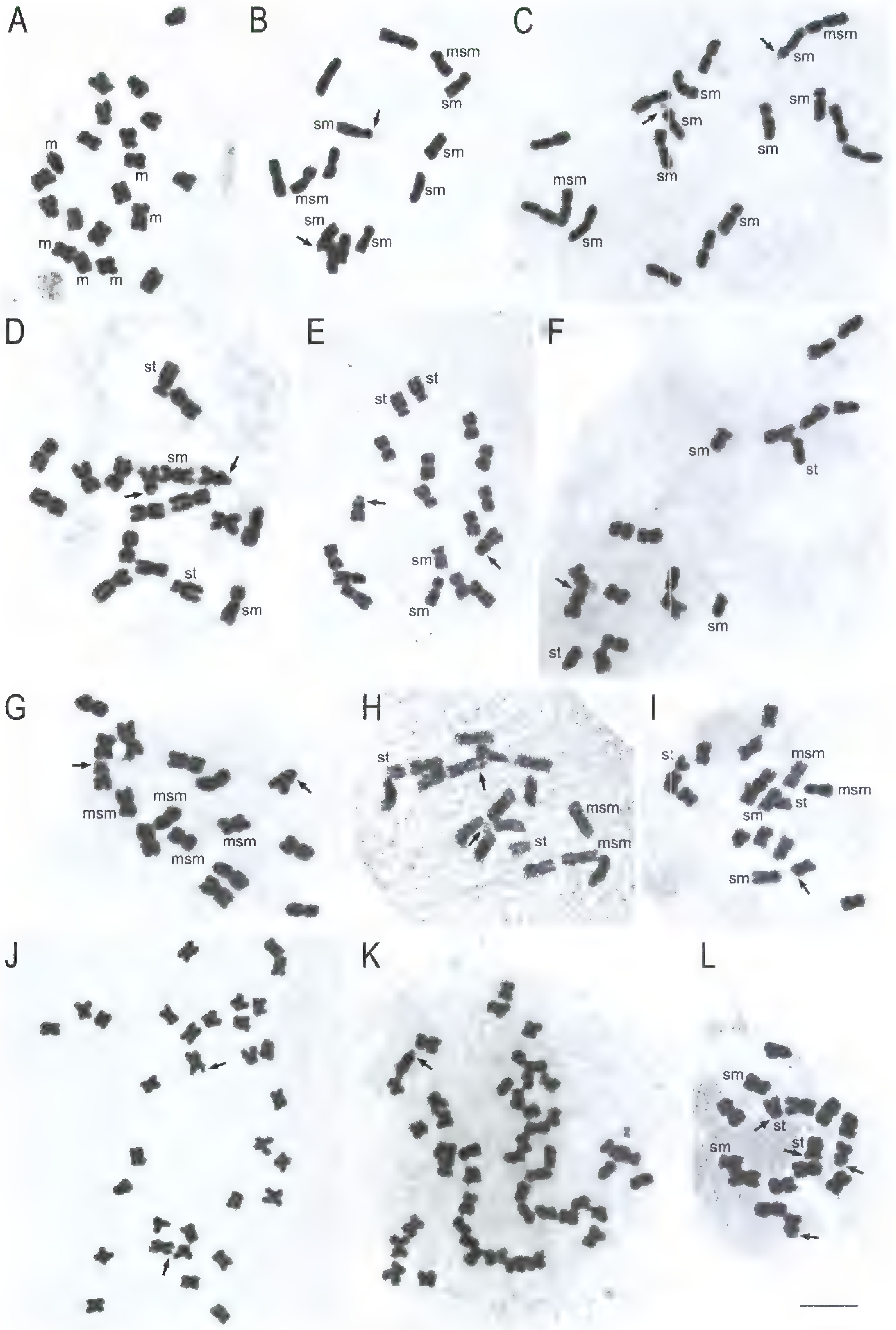

Figure 1. Somatic metaphases of *Leptoglossis*, *Petunia*, *Fabiana*, *Nierembergia*, and *Bouchetia* species. —A. *L. linifolia* ($2n = 20$). —B. *P. axillaris* ($2n = 14$). —C. *P. patagonica* ($2n = 18$). —D. *F. densa* ($2n = 18$). —E. *F. denudata* ($2n = 18$). —F. *F. imbricata* ($2n = 18$). —G. *N. browallioides* ($2n = 16$). —H. *N. ericoides* ($2n = 18$). —I. *N. scoparia* ($2n = 18$). —J. *N. rigida* ($2n = 32$). —K. *N. aristata* ($2n = 48$). —L. *B. anomala* ($2n = 16$). Arrows (↑) indicate nucleolar organizing regions (NORs). Less frequent chromosome types are indicated: *m*, metacentric; *msm*, meta-submetacentric; *sm*, submetacentric; *st*, subtelocentric. Scale bar = 5 μm is the same for all figures.

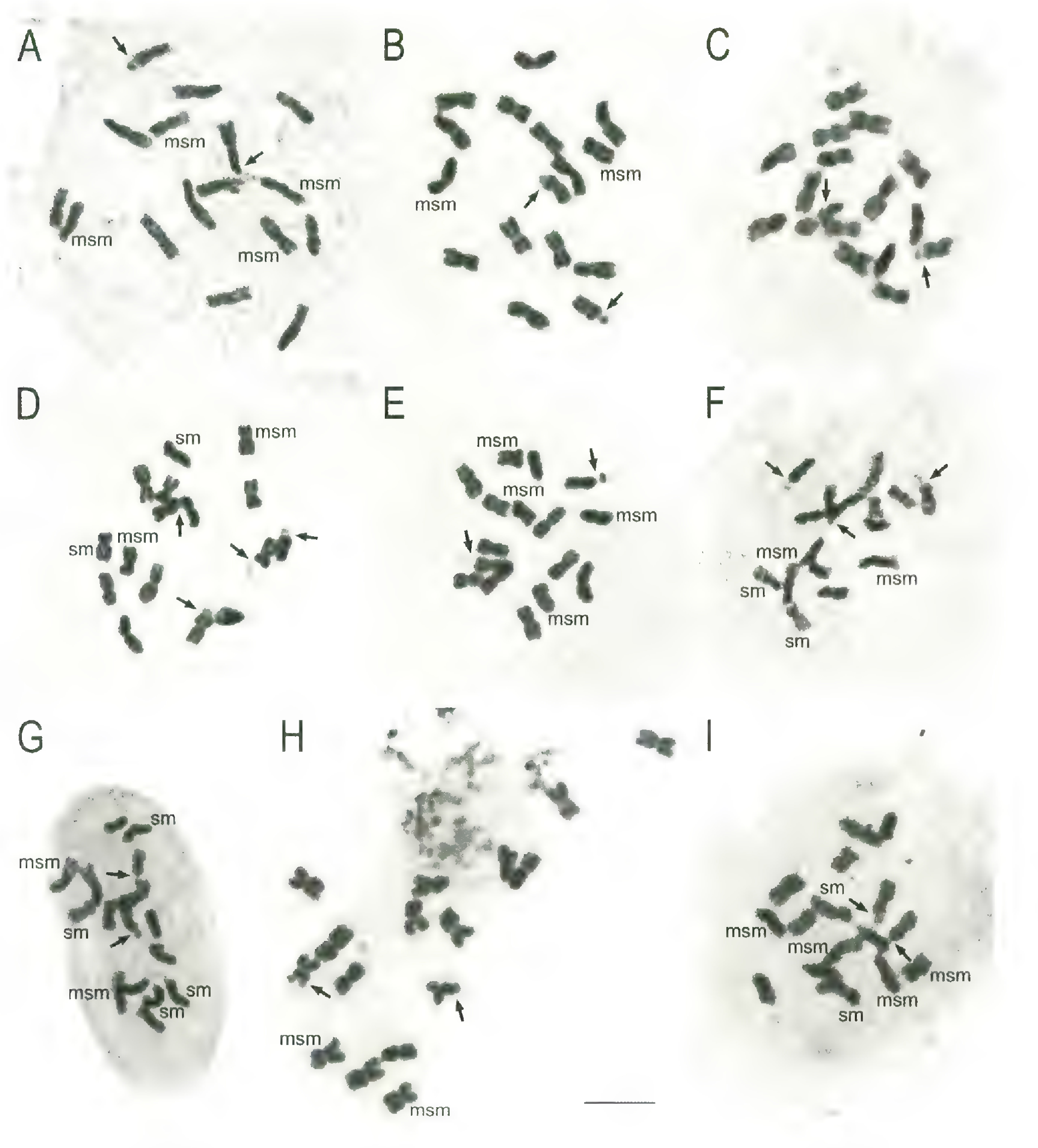

Figure 2. Somatic metaphases of *Nierembergia* species with $2n = 16$. —A. *N. calycina*. —B. *N. pulchella* var. *pulchella*. —C. *N. pulchella* var. *macrocalyx*. —D. *N. graveolens*. —E. *N. linariifolia* var. *pinifolioides*. —F. *N. repens*. —G. *N. rivularis*. —H. *N. tucumanensis*. —I. *N. veitchii*. Arrows (↑) indicate nucleolar organizing regions (NORs). Less frequent chromosome types are indicated: *msm*, meta-submetacentric; *sm*, submetacentric. Scale bar = 5 μm is the same for all figures.

chromosome number changes in the series of Nicotianeae in the context of the family. The pivotal position of $x = 11$ is noteworthy; thus, this number could represent a plesiomorphic state in Solanaceae. This basic number is dominant in the basal branching of the family (subfam. Salpiglossoideae (Benth.) Hunz. and tribe Browallieae), except for the earliest diverging lineages of *Schizanthus* Ruiz & Pav. (subfam. Schizanthoideae (Miers) Hunz.) and *Schwenckia* (subfam. Schwenckieae), both genera displaying $x = 10$, which may be derived by a decrease in chromosome number. In addition, $x = 11$ is the number of the suspected primitive Benthamielleae (Hunz.) Hunz. (Cestroideae) (Moscone, 1989a; Hunziker, 2001), a taxon not included in the molecular studies by Olmstead & Palmer (1992) and Olmstead et al. (1999). Reduction in chromosome number could also account for the appearance of $x = 8$ in all Cestreae, whose members are in a group sister to Browallieae, where $x = 11$ is typical (see Olmstead et al., 1999: figs. 3, 4).

Among the Nicotianeae, chromosomal reduction is also suggested by the presence of $x = 9$ in *Fabiana* and *Petunia*, both taxa forming a sister lineage to the tribe Franciseeae G. Don (Cestroideae) with $x = 11$, and of $x = 10$ in *Leptoglossis*, a genus molecularly not

examined by Olmstead & Palmer (1992) and Olmstead et al. (1999). Further decrease from $x = 9$ to $x = 7$ in *Petunia* and to $x = 8$ in the monophyletic group composed of *Bouchetia*, *Hunzikeria*, and *Nierembergia* (see Olmstead et al., 1999: figs. 1, 2) could have occurred. Under this scheme, the rare $x = 9$ in the latter genus may be a dysploid increase from $x = 8$.

Finally, $x = 12$, almost universal in the monophyletic and derived cluster comprising *Nicotiana*, Solanoideae Schltdl., and Juanulloideae (Hunz.) Hunz. (Olmstead & Palmer, 1992; Olmstead et al., 1999), could have arisen by an increase from $x = 11$. Particularly in *Nicotiana*, all other basic numbers should be derived from $x = 12$, because they are restricted to sections *Suaveolentes* and *Alatae*, with the former group being a species assemblage geographically isolated and most probably derived (Goodspeed, 1954; Aoki & Ito, 2000). Additional chromosome and molecular data are needed to test these speculations.

POLYPLOIDY

All Nicotianeae species studied are diploids, although *Nierembergia rigida* and *N. aristata* also show tetraploid and hexaploid cytotypes, respectively. The presence of infraspecific polyploidy in the former species was unknown, while in the latter, Di Fulvio (1984) has cited the same levels of ploidy as reported here. Although polyploidy has played a significant role in the evolution of *Nicotiana*, where many species are amphidiploids (Chase et al., 2003), it does not appear to be relevant in the remaining genera of Nicotianeae as so far reported just for *Petunia spathulata* L. B. Sm. & Downs ($n = 18$; Stehmann et al., 1997) and *Hunzikeria texana* (Torr.) D'Arcy ($n = 16$; Whalen, 1979), in addition to the aforementioned species of *Nierembergia*. In the case of the hexaploid accession *Acosta et al. 32* (CORD) of *Nierembergia aristata*, the presence of multivalent configurations (particularly hexavalents) in meiosis suggests an autopolyploid origin. Concerning the polyploid samples *Subils et al. 4215* (CORD) of *N. aristata* and *Cocucci et al. 943* (CORD) of *N. rigida*, although they show a smaller number of NORs than expected (just one pair), they could have arisen by autopolyploidy, as suggested by Di Fulvio (1984) for another polyploid accession of the first species. The increased size of plant organs and structures in those populations compared to diploid counterparts in both species, and also reported previously for *N. aristata* (Di Fulvio, 1984), corresponds to the gigas phenotype more frequently present in autopolyploids than in allopolyploids (Singh, 1993). Further karyotypic and meiotic analyses of the polyploid samples here studied are required to cast light on their origin.

Both *Nierembergia* species with polyploid cytotypes have wide geographical distributions, although the hexaploid accessions of *N. aristata* in particular grow in flooded regions, while the tetraploid population of *N. rigida* occur in hilly habitats modified by man. The capability of polyploids to tolerate harsh ecological conditions and colonize disturbed habitats is well known (Stebbins, 1966, 1980). In particular, the population *Acosta et al. 32* of *N. aristata* seems to be of recent origin, because its ecological niche, at the border of a lake, arose about 100 years ago with the building of a dam in the region (Di Fulvio, 1984). The derived condition of polyploidy in *Nierembergia* is suggested by the fact that diploid complements are widespread in the genus.

SYSTEMATICS AND KARYOTYPE EVOLUTION

The results of the present work suggest that the species of *Nierembergia* can be grouped according to their karyotype features. Among the entities with $2n = 16$, two groups are distinguished. One of them, group I, is composed of *N. browallioides*, *N. calycina*, *N. linariifolia*, *N. pulchella*, and *N. tucumanensis*, with comparatively large chromosomes and more symmetrical karyotypes, composed only of *m* pairs or mainly of *m* and one to two *msm* pairs. It should be noted that *N. calycina* is the only species with NORs on long chromosome arms, perhaps as a result of an inversion; thus, it stands apart in group I. The other group (II) consists of *N. aristata*, *N. graveolens*, *N. repens*, *N. rigida*, *N. rivularis*, and *N. veitchii*, with smaller chromosomes and more asymmetrical complements, where one to two *sm* in addition to one to two *msm* pairs or three *msm* pairs are present. Finally, the species having $2n = 18$, *N. ericoides* and *N. scoparia*, form a third group (III), characterized by a small *st* chromosome pair. This grouping is supported by external morphology, reproductive biology, habit, and habitat affinities. The taxa included in groups I and III are small shrubs (except *N. calycina*, which is an herb), usually of mountain habitats, with single pollen grains and a semilunar stigma. On the other hand, group II is composed of rhizomatous, stoloniferous or tuber-bearing, and creeping herbs, except for the shrubby *N. graveolens*. These taxa grow in lowland habitats and are characterized by aggregates of pollen grains (except *N. graveolens* with single pollen grains) and a capitate stigma (Di Fulvio, 1976b; Cocucci & Hunziker, 1995).

In group III, $2n = 18$ seems to be a derived condition, because $2n = 16$ is present in most *Nierembergia* species and also in the related genus

Bouchetia. This variation in basic chromosome number could have arisen by a centric fission event during species diversification as has been postulated in other Solanaceae (Moscone et al., 1993). This hypothesis is supported by the presence of an additional small *st* chromosome pair in the taxa with $2n = 18$. On the other hand, group II, with morphological specializations such as much reduced branching, more pronounced zygomorphy (in part), and increased karyotype asymmetry, appears to have an advanced status relative to group I (Cocucci & Hunziker, 1995).

The similar karyotypes in the shrubby species of *Fabiana* studied is striking because the plants are morphologically very different from each other, i.e., *F. imbricata*, tall with comparatively imbricate leaves and conspicuous flowers, as well as *F. densa* and *F. denudata*, both comparatively small, but the former with a dense foliage of linear leaves and the latter nearly without leaves (Barboza & Hunziker, 1993). In *Petunia*, both species studied differ in chromosome number but not in karyotype asymmetry. In particular, *P. axillaris* has a similar karyotype to *P. hybrida* (Hook.) Vilm., another member of *Petunia* sensu Wijsman (1990) (a group with $x = 7$). On the other hand, the chromosome complement of *P. patagonica* does not differ from that of *P. linearis* (Hook.) Paxt., a species from the group with $x = 9$, which is now considered as *Calibrachoa* (Wijsman et al., 1983; Maizonnier, 1984). Chromosome features together with morphological traits, such as the corolla not entirely single colored and calyx lobes pentafid and not deeply incised, indicate that *P. patagonica* should be included in the *Calibrachoa* group (Wijsman & de Jong, 1985; Figueroa Romero, 1993; Mishiba et al., 2000). In general, *Petunia* sensu Wijsman displays advanced morphological features in comparison to *Calibrachoa* and the related genus *Fabiana*, as it comprises annual herbs without woody stems and brachyblasts (Barboza & Hunziker, 1993; Kulcheski et al., 2006).

The present results demonstrate that some genera of Nicotianeae, i.e., *Fabiana*, *Nierembergia*, and *Petunia*, display general karyotype patterns where uniformity in gross chromosome morphology (i.e., similar chromosome shape between taxa) is maintained even after changes in chromosome number. This occurs in several sections of *Nicotiana* (Goodspeed, 1954). Species-wide karyotypic orthoselection concerning both chromosome number and morphology has been observed in other genera of Solanaceae (e.g., *Cestrum*, *Capsicum* L., and *Solanum* L.) and other plant groups including an entire angiosperm family, as in the case of the Aloaceae (Moscone, 1989b; Bernardello & Anderson, 1990; Moscone et al., 1993; Brandham & Doherty, 1998).

Karyotypic data suggest that *Bouchetia*, with $x = 8$ and a rather symmetrical karyotype in the case of *B. anomala*, is closely related to *Nierembergia*. On the other hand, *Leptoglossis*, *Petunia*, and *Fabiana*, without $x = 8$ and with more asymmetrical complements except in the latter genus, appear more distant, in agreement with the suprageneric classification proposed by Hunziker (2001). Finally, the basic chromosome number recorded for *Hunzikeria* ($x = 8$) indicates affinity to *Bouchetia* and *Nierembergia* and a more distant relationship to *Leptoglossis*, in disagreement with Hunziker's (2001) system.

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CHROMOSOME STUDIES IN AMERICAN PANICOIDEAE (POACEAE)[1]

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Abstract

Chromosome numbers and observations on meiotic chromosome behavior of 37 taxa of American Panicoideae are given. The taxa studied are: *Axonopus scoparius* (Flüggé) Kuhlm., *Cenchrus myosuroides* Kunth, *Dichanthelium aciculare* var. *aciculare* (Desv. ex Poir.) Gould & C. A. Clark, *D. acuminatum* var. *acuminatum* (Sw.) Gould & C. A. Clark, *Echinochloa chacoensis* P. W. Michael ex Renvoize, *Eriochloa montevidensis* Griseb., *Isachne arundinacea* (Sw.) Griseb., *Panicum hirticaule* J. Presl, *P. stoloniferum* Poir., *P. trichanthum* Nees, *Paspalum blodgettii* Chapm., *P. buchtienii* Hack., *P. caespitosum* Flüggé, *P. candidum* (Humb. & Bonpl. ex Flüggé) Kunth, *P. ceresia* (Kuntze) Chase, *P. clavuliferum* C. Wright, *P. commune* Lillo, *P. denticulatum* Trin., *P. ekmanianum* Henrard, *P. ellipticum* Döll, *P. fimbriatum* Kunth, *P. glabrinode* (Hack.) Morrone & Zuloaga, *P. glaucescens* Hack., *P. hartwegianum* E. Fourn., *P. inconstans* Chase, *P. indecorum* Mez, *P. juergensii* Hack., *P. pauciciliatum* (Parodi) Herter, *P. penicillatum* Hook. f., *P. plicatulum* Michx., *P. prostratum* Scribn. & Merr., *P. saccharoides* Nees ex Trin., *P. squamulatum* E. Fourn., *P. variabile* (E. Fourn.) Nash, *P. wrightii* Hitchc. & Chase, *Urochloa fusca* (Sw.) B. F. Hansen & Wunderlin, and *U. lorentziana* (Mez) Morrone & Zuloaga. Nine counts are first reports for *Echinochloa chacoensis* ($2n$ = ca. 72), *Panicum stoloniferum* ($2n = 20$), *Paspalum buchtienii* ($2n = 20$), *P. ceresia* ($2n = 40$), *P. ekmanianum* ($2n = 20$), *P. glabrinode* ($2n = 20$), *P. inconstans* ($2n$ = ca. 60), *P. penicillatum* ($2n = 40$), and *P. variabile* ($2n = 40$). Ten counts differed from previously published counts: *Axonopus scoparius* ($2n = 60$), *Cenchrus myosuroides* ($2n$ = ca. 72), *Isachne arundinacea* ($2n = 20$), *Paspalum denticulatum* ($2n = 20$), *P. ellipticum* ($2n = 40$), *P. fimbriatum* ($2n$ = ca. 40), *P. hartwegianum* ($2n = 40$), *P. saccharoides* ($2n = 40$), *P. squamulatum* ($2n = 20$), and *Urochloa lorentziana* ($2n = 36$).

Key words: America, chromosome numbers, Panicoideae, Poaceae.

Knowledge of chromosome numbers and their meiotic behavior is important for understanding the phylogeny of vascular plants (Raven, 1975), particularly with regard to polyploid taxa (Davidse et al., 1986). Polyploidy is a common feature in the Poaceae, but karyological studies are still lacking in many tropical and subtropical grasses (Honfi et al., 1991), limiting our ability to understand the patterns of chromosome number change across the family. In addition, knowledge of the relationship between polyploidy and apomixis in tropical genera of grasses, such as *Dichanthelium* (Hitchc. & Chase) Gould, *Panicum* L., *Paspalum* L., and *Urochloa* P. Beauv., is necessary for plant breeding programs and for studies of reproductive systems (Connor, 1979; Quarín & Norrmann, 1987; Honfi et al., 1991; Norrmann et al., 1994).

The purpose of this work is to increase the cytological knowledge of species of Panicoideae collected in different regions of America. Chromosome counts were made in taxa of the tribe Isachneae (*Isachne*) and Paniceae (*Axonopus* P. Beauv., *Cenchrus* L., *Dichanthelium*, *Echinochloa* P. Beauv., *Eriochloa* Kunth, *Panicum*, *Paspalum*, and *Urochloa*). Chromosome numbers were compared with previous results published in the Poaceae, including the following indexes: Ornduff (1967, 1968, 1969), Bolkhovskikh et al. (1969), Moore (1970, 1971, 1972, 1973, 1974, 1977), Goldblatt (1981, 1984, 1985, 1988), and Goldblatt and Johnson (1990, 1991, 1994, 1996, 1998, 2000).

Material and Methods

Meiosis was studied in five to 10 pollen mother cells per sample. All counts but one here reported were made from meiotic material fixed in the field with Carnoy's solution (6 parts ethanol:3 chloroform:1 acetic acid); chromosomes were stained with 2% iron propionic haematoxylin (Sáez, 1960; Núñez, 1968) and with 2% acetic carmine. Permanent slides were obtained by the dry method or by Bradley's technique (i.e., slides are dehydrated in absolute alcohol and mounted in Euparal) (Bradley, 1948). A complete list of the species, chromosome numbers, and voucher specimens studied is given in Table 1.

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Table 1. Chromosome numbers and configuration chromosome associations in taxa of American Panicoideae. *Taxa not previously cytologically studied. **Taxa with chromosome numbers that differ from previously published reports.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
***Axonopus scoparius* (Flüggé) Kuhlm.	30 II	BOLIVIA. La Paz: Prov. Nor Yungas, camino Los Yungas, alrededores de Coroico, *Morrone et al. 4209* (LPB, SI).
***Cenchrus myosuroides* Kunth	ca. 36	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, de Aeropuerto El Cadillal a SS de Jujuy, *Zuloaga & Morrone 7049* (MO, SI).
Dichanthelium aciculare var. *aciculare* (Desv. ex Poir.) Gould & C. A. Clark	9 II	MEXICO. Veracruz: Carretera 140 de Xalapa a Perote, El Acajete, *Zuloaga et al. 7442* (MEXU, SI).
Dichanthelium aciculare var. *aciculare* (Desv. ex Poir.) Gould & C. A. Clark	9 II	MEXICO. Oaxaca: Carretera de San Jerónimo a Huautla, 22 km W de Huautla, *Zuloaga et al. 7395* (MEXU, SI).
Dichanthelium acuminatum var. *acuminatum* (Sw.) Gould & C. A. Clark	9 II	MEXICO. Oaxaca: Carretera de San Jerónimo a Huautla, 22 km W de Huautla, *Zuloaga et al. 7392* (MEXU, SI).
**Echinochloa chacoensis* P. W. Michael ex Renvoize	ca. 36 II	ARGENTINA. Jujuy: Dpto. Palpalá, Ruta el algarrobal a El Cucho, *Zuloaga et al. 5848* (MO, SI).
Eriochloa montevidensis Griseb.	18 II	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, Zapla, Mina 9 de Octubre, *Morrone et al. 4422* (MO, SI).
***Isachne arundinacea* (Sw.) Griseb.	10 II	BOLIVIA. La Paz: Prov. Sud Yungas, camino Los Yungas, a 57 km de La Paz camino a Coroico, *Morrone et al. 4192* (LPB, SI).
Panicum hirticaule J. Presl	9 II	MEXICO. Michoacán: Ruta 110, camino a Zamora pasando Villarrica, *Morrone & Giussani 3641* (MEXU, SI).
**Panicum stoloniferum* Poir.	10 II	BOLIVIA. Santa Cruz: Prov. Andrés Ibañez, 58 km de S. Cruz camino a Samaipata, *Morrone & Giussani 4268* (LPB, SI).
Panicum trichanthum Nees	18 II	ARGENTINA. Jujuy: Dpto. Santa Bárbara, 21 km de Palma Sola camino a Puesto Maíz Gordo, *Morrone et al. 4451* (MO, SI).
Paspalum blodgettii Chapm.	20 II	MEXICO. Quintana Roo: Ruta Mex-307, 43 km al S de Playa del Carmen a Tulum, *Morrone & Giussani 3658* (MEXU, SI).
**Paspalum buchtienii* Hack.	$2n = 20$	BOLIVIA. Santa Cruz: Prov. Andrés Ibañez, 58 km de Santa Cruz camino a Samaipata, *Morrone & Giussani 4258* (LPB, SI).
**Paspalum buchtienii* Hack.	10 II	BOLIVIA. La Paz: Prov. Nor Yungas, camino Los Yungas, a 63 km de La Paz camino a Coroico, *Morrone et al. 4201* (LPB, SI).
Paspalum caespitum Flüggé	10 II	MEXICO. Quintana Roo: Ruta Mex-307, 43 km al S de Playa del Carmen a Tulum, *Morrone & Giussani 3656* (MEXU, SI).
Paspalum candidum (Humb. & Bonpl. ex Flüggé) Kunth	30 II 28 II + 4 I	MEXICO. Oaxaca: San Jerónimo, *Zuloaga et al. 7396* (MEXU, SI).
**Paspalum ceresia* (Kuntze) Chase	20 II	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, 10 km de León camino a Tiraxi, *Morrone et al. 4386* (MO, SI).
Paspalum clavuliferum C. Wright	10 II	BRAZIL. Bahia: Mun. Mucugé, BA-142, de Mucugé a Barra da Estiva, 6 km de Mucugé, *Zuloaga & Morrone 6978* (MO, SI).

Table 1. Continued.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
Paspalum commune Lillo	20 II 19 II + 2 I	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, Zapla, Mina 9 de Octubre, *Morrone et al. 4420* (MO, SI).
***Paspalum denticulatum* Trin.	10 II	MEXICO. Puebla: Carretera de Tehuacán a Zapotitlán, km 10, cerca de Marmolera, *Zuloaga et al. 7384* (MEXU, SI).
**Paspalum ekmanianum* Henrard	10 II	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, Palpalá, Mina 9 de Octubre, *Zuloaga et al. 5852* (MO, SI).
***Paspalum ellipticum* Döll	20 II	BRAZIL. Goiás: Alto Paraiso, *Filgueiras 3517* (IBGE, SI).
***Paspalum fimbriatum* Kunth	ca. 20 II ca. 19 II + 2 I ca. 16 II + 8 I	MEXICO. Quintana Roo: Mun. Cozumel, Isla de Cozumel, Laguna Chankanaab, *Morrone & Giussani 3651* (MEXU, SI).
**Paspalum glabrinode* (Hack.) Morrone & Zuloaga	10 II	ARGENTINA. Misiones: Dpto. San Ignacio, Peñón de La Reina Victoria, *Zuloaga & Morrone 6809* (MO, SI).
Paspalum glaucescens Hack.	20 II 19 II + 2 I 18 II + 4 I 2 IV + 13 II + 6 I	ARGENTINA. Formosa: Ruta Nac. 11, de Clorinda a Formosa, *Zuloaga & Morrone 7337* (MO, SI).
***Paspalum hartwegianum* E. Fourn.	20 II	MEXICO. Michoacán: Ruta 15d, km 159, pasando el Mun. de Maravatio, Puente Satire, *Morrone & Giussani 3612* (MEXU, SI).
**Paspalum inconstans* Chase	ca. 30 II	BOLIVIA. La Paz: Prov. Sud Yungas, camino Los Yungas, a 56 km de La Paz camino a Coroico, *Morrone et al. 4190* (LPB, SI).
Paspalum indecorum Mez	$2n = 20$	ARGENTINA. Misiones: Dpto. Capital, Ruta Nac. 105, de Posadas a San José, *Zuloaga & Morrone 7142* (MO, SI).
Paspalum juergensii Hack.	10 II	BOLIVIA. La Paz: Prov. Sud Yungas, a 56 km de La Paz camino a Coroico, *Morrone et al. 4188* (LPB, SI).
Paspalum pauciciliatum (Parodi) Herter	$2n =$ ca. 38	ARGENTINA. Misiones: Dpto. San Ignacio, Jardín América, *Zuloaga & Morrone 7191* (MO, SI).
**Paspalum penicillatum* Hook. f.	ca. 20 II 18 II + 4 I	BOLIVIA. La Paz: Prov. Sud Yungas, camino Los Yungas, a 57 km de La Paz camino a Coroico, *Morrone et al. 4200* (LPB, SI).
Paspalum plicatulum Michx.	10 II	MEXICO. Veracruz: Autopista de La Isla a Acayucán, km 66, *Zuloaga et al. 7418* (MEXU, SI).
Paspalum prostratum Scribn. & Merr.	ca. 20 II	MEXICO. Puebla: Carretera de Teotitlán a Huauclan, 20 km de Teotitlán, *Zuloaga et al. 7387* (MEXU, SI).
***Paspalum saccharoides* Nees ex Trin.	20 II	BOLIVIA. La Paz: Nor Yungas, a 23 km de Yolosa camino hacia Caranavi, *Morrone et al. 4211* (LPB, SI).
***Paspalum squamulatum* E. Fourn.	10 II	MEXICO. Oaxaca: Carretera de San Jerónimo a Huautla, 22 km W de Huautla, *Zuloaga et al. 7389* (MEXU, SI).
Paspalum squamulatum E. Fourn.	20 II	MEXICO. Veracruz: Carretera 140 de Xalapa a Perote, El Acajete, *Zuloaga et al. 7443* (MEXU, SI).

Table 1. Continued.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
**Paspalum variabile* (E. Fourn.) Nash	20 II 19 II + 2 I	MEXICO. Oaxaca: Carretera entre San Jerónimo y Huautla, 12 km de Huautla, *Zuloaga et al. 7397* (MEXU, SI).
Paspalum wrightii Hitchc. & Chase	10 II	MEXICO. Oaxaca: Carretera Tuxtepec a Loma Bonita, 20 km de Tuxtepec, *Zuloaga et al. 7411* (MEXU, SI).
Urochloa fusca (Sw.) B. F. Hansen & Wunderlin	9 II	ARGENTINA. Jujuy: Dpto. Ledesma, Ruta Prov. 31, 7 km del desvío de la Ruta Prov. 1 camino a Vinalito, *Morrone et al. 2914* (MO, SI).
***Urochloa lorentziana* (Mez) Morrone & Zuloaga	18 II	ARGENTINA. Tucumán: Dpto. Trancas, Ruta Nac. 9, 80 km de R. de la Frontera camino a S.M. de Tucumán, *Morrone et al. 4653* (MO, SI).

Voucher specimens were deposited at the Instituto de Botánica Darwinion (SI), with duplicates at LPB, MEXU, and MO.

Results and Discussion

All studied species are summarized in Table 1, including the examined configurations, voucher specimens, their provenance, and the respective collector. Collections are alphabetically ordered by genus and species and are discussed below in that order. Photomicrographs of selected species are shown in Figures 1 and 2.

Most results agreed with previously published chromosome numbers, but our counts differed for 10 species; these taxa were *Axonopus scoparius* (Flüggé) Kuhlm. ($2n = 60$), *Cenchrus myosuroides* Kunth ($2n =$ ca. 72), *Isachne arundinacea* (Sw.) Griseb. ($2n = 20$), *Paspalum denticulatum* Trin. ($2n = 20$), *P. ellipticum* Döll ($2n = 40$), *P. fimbriatum* Kunth ($2n =$ ca. 40), *P. hartwegianum* E. Fourn. ($2n = 40$), *P. saccharoides* Nees ex Trin. ($2n = 40$), *P. squamulatum* E. Fourn. ($2n = 20$), and *Urochloa lorentziana* (Mez) Morrone & Zuloaga ($2n = 36$).

Nine additional species were previously unknown cytogenetically. These first reports for chromosome number are: *Echinochloa chacoensis* P. W. Michael ex Renvoize ($2n =$ ca. 72), *Panicum stoloniferum* Poir. ($2n = 20$), *Paspalum buchtienii* Hack. ($2n = 20$), *P. ceresia* (Kuntze) Chase ($2n = 40$), *P. ekmanianum* Henrard ($2n = 20$), *P. glabrinode* (Hack.) Morrone & Zuloaga ($2n = 20$), *P. inconstans* Chase ($2n =$ ca. 60), *P. penicillatum* Hook. f. ($2n = 40$), and *P. variabile* (E. Fourn.) Nash ($2n = 40$).

Axonopus scoparius, a species of the series Barbigeri, subseries Scoparii (sensu Black, 1963), is an important natural forage grass in the Andean region. The specimen studied, from Bolivia, is a hexaploid with a count of $2n = 60$ (Fig. 1A), which differs from previous counts published by Pohl and Davidse (1971) and Shibata (1962), who reported $2n = 20$ for this species.

The widespread genus *Cenchrus*, with approximately 20 pantropical species, has base chromosome numbers of $x = 9$, 10, and 17 (Núñez, 1952; DeLisle, 1963). *Cenchrus myosuroides* has $2n =$ ca. 72, a number which differs from previous reports for this species: $2n = 54$ (Brown, 1950), $2n =$ ca. 68 (Bowden & Senn, 1962), and $2n = 70$ (Parodi, 1946; Gould, 1965; Reeder, 1968).

The American genus *Dichanthelium* includes several polymorphic complexes of uncertain specific delimitation, with different foliar and floral dimorphisms correlated with seasonal variability (Gould & Clark, 1978; Zuloaga et al., 1993). A high percentage of diploids, approximately 80%, have been reported for North and Central American species of *Dichanthelium* (Dubcovsky & Zuloaga, 1991). The genus has a base chromosome number of $x = 9$ (Brown, 1948; Gould, 1966, 1968), and the chromosome counts for *D. aciculare* (Desv. ex Poir.) Gould & C. A. Clark and *D. acuminatum* (Sw.) Gould & C. A. Clark, based on Mexican specimens, are diploid with $2n = 18$, a result that confirms previous reports for these species (Brown, 1948; Gould, 1958; Dubcovsky & Zuloaga, 1991, cited under the genus *Panicum*).

The genus *Echinochloa* includes nearly 40 species, many of them dominant in wetlands or in disturbed open areas, including cultivated fields, of tropical and temperate zones. *Echinochloa chacoensis*, a species restricted to eastern Bolivia and northern Argentina, is an octoploid with $2n =$ ca. 72, the first count for

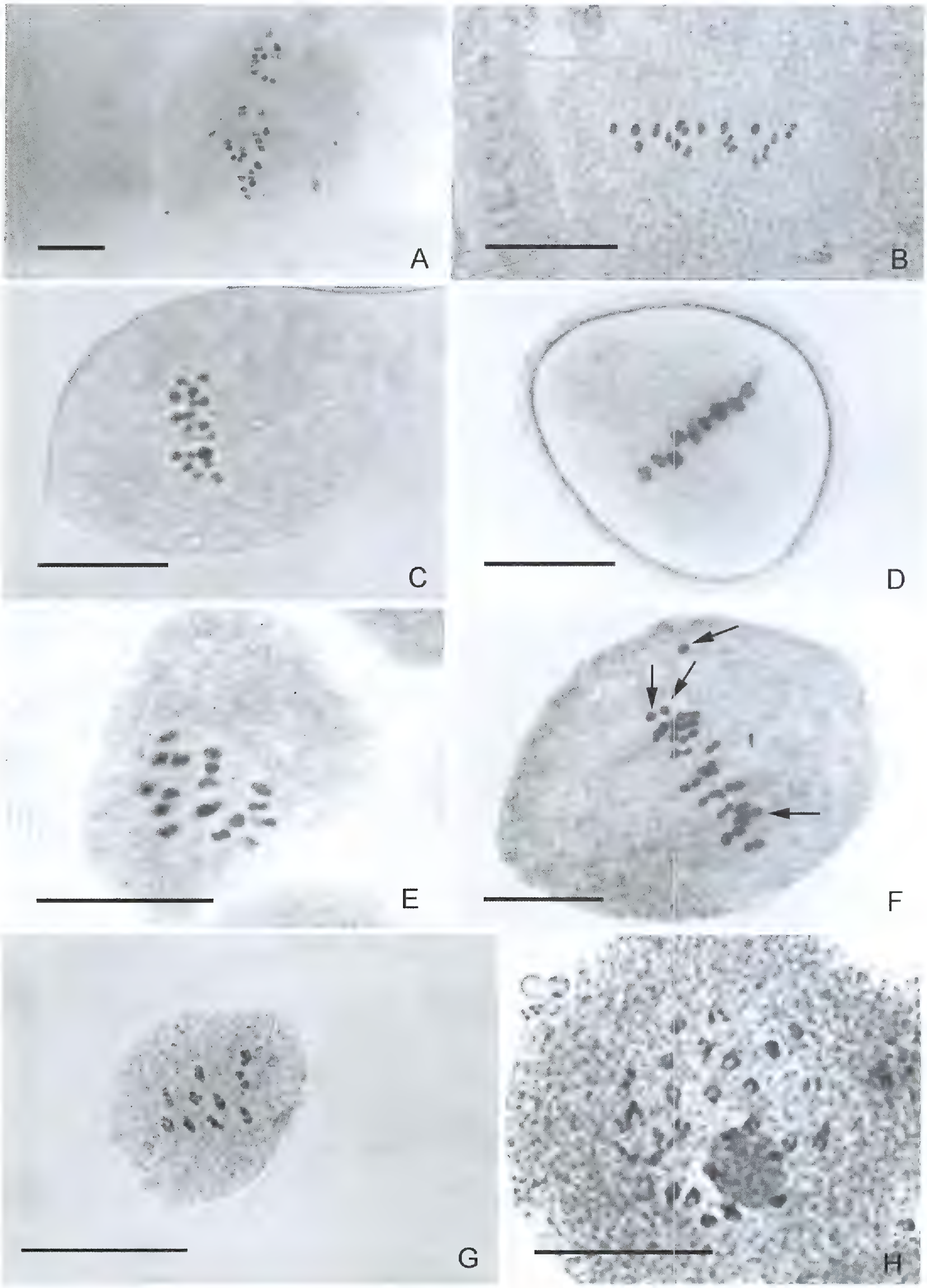

Figure 1. Photomicrographs of meiotic chromosomes of American Panicoideae. —A. *Axonopus scoparius*, 30 II, metaphase I. —B. *Eriochloa monteridensis*, 18 II, metaphase I. —C. *Panicum stoloniferum*, 10 II, prometaphase I. —D. *Paspalum glabrinode*, 10 II, metaphase I. —E. *Panicum trichanthum*, 18 II, prometaphase I. —F. *Paspalum penicillatum*, 18 II + 4 I, metaphase I. —G. *Paspalum denticulatum*, 10 II, prometaphase I. —H. *Paspalum candidum*, 30 II, diakinesis. Arrows show univalents. Scale bar = 20 μm.

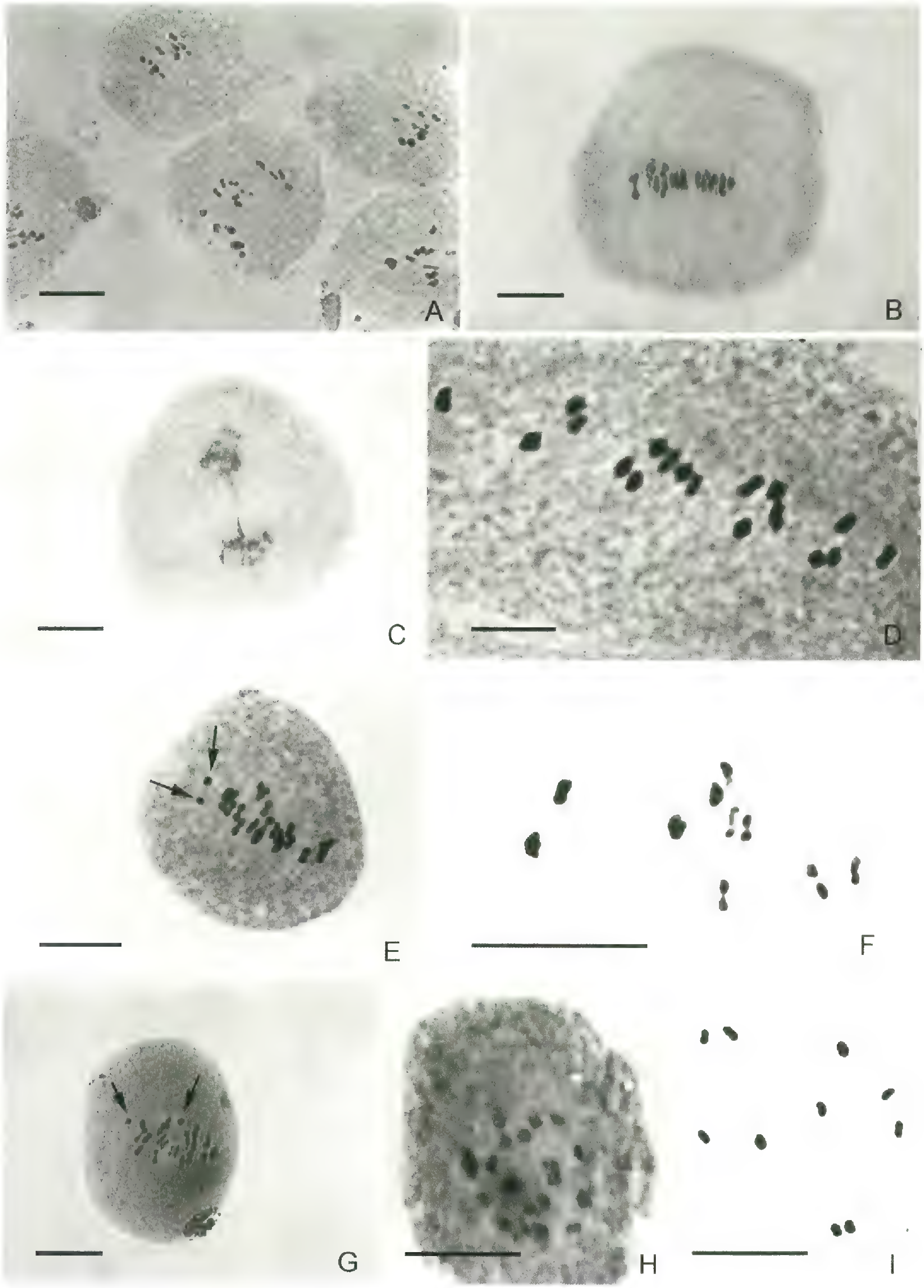

Figure 2. Photomicrographs of meiotic chromosomes of American Panicoideae. —A. *Paspalum buchtienii*, 10 II, prometaphase I. —B. *Paspalum ceresia*, 20 II, metaphase I. —C. *Paspalum commune*, bridge at anaphase II. —D. *Urochloa lorentziana*, 18 II, metaphase I. —E. *Paspalum glaucescens*, 19 II + 2 I, prometaphase I. —F. *Paspalum ekmanianum*, 10 II, metaphase I. —G. *Paspalum variabile*, 18 II + 2 I, prometaphase I. —H. *Paspalum prostratum*, ca. 20 II, diakinesis. —I. *Paspalum plicatulum*, 10 II, prometaphase I. Arrows show univalents. Scale bar = 20 μm.

this species. Polyploidy is common in *Echinochloa*, but octoploids had not been previously documented in the genus.

Eriochloa is a cosmopolitan genus with ca. 30 species present in open habitats of all continents; tetraploids, hexaploids, and octoploids have been reported in the genus. *Eriochloa montevidensis* Griseb. is a tetraploid with $2n = 36$ (Fig. 1B), a chromosome count that agrees with a previous count for the species (Núñez in Parodi, 1946); it should be mentioned that there is also a diploid count of $2n = 18$ for this species (Pohl & Davidse, 1971).

Within the pantropical genus *Isachne*, the count of a Bolivian *I. arundinacea* specimen was diploid with $2n = 20$, which differs from other published counts for this species that found individuals with $2n = 40$ (Tateoka, 1962; Davidse & Pohl, 1974).

Panicum hirticaule J. Presl, a species of subgenus *Panicum* (Zuloaga & Morrone, 1996), is a diploid with $2n = 18$, in agreement with previous results for this species (Fairbrothers, 1954; Gould, 1965; Davidse & Pohl, 1972b).

Section *Stolonifera* Hitchc. & Chase ex Pilg. of *Panicum* includes 13 American species found in the interior or at the edges of forests (Zuloaga, 1987; Zuloaga & Sendulsky, 1988). This section has been characterized as having a base chromosome number of $x = 10$, based on studies of *P. pulchellum* Raddi (Gould & Soderstrom, 1970; Pohl & Davidse, 1971; Davidse & Pohl, 1974). We here present the first chromosome count for *P. stoloniferum*, based on a specimen from Bolivia with a diploid number of $2n = 20$ (Fig. 1C).

Section *Parvifolia* Hitchc. & Chase ex Pilg. of *Panicum* has a base chromosome number of $x = 9$ (Zuloaga, 1987). A total of 31 species, found in open and moist places, are recognized from America within this section (Aliscioni et al., 2003). *Panicum trichanthum* Nees is a tetraploid with $2n = 36$ (Fig. 1E), which confirms previous counts for this species (Pohl & Davidse, 1971; Davidse & Pohl, 1972a, b, 1978; Honfi et al., 1991).

The genus *Paspalum* has approximately 310 species that are primarily American, and most have a base chromosome number of $x = 10$ (Burson, 1975). Many of these are polyploid, but most are tetraploid (Pagliarini et al., 2001). A total of 25 species were studied; of the counts recorded, 14 are new or differ from previously reported counts. Of these 25 species, 13 were tetraploids, 10 were diploids, and two were hexaploids. Chase (1929, ined.) and Zuloaga and Morrone (2005) are followed for the infrageneric arrangement of species.

Diploidy ($2n = 20$), tetraploidy ($2n = 40$), hexaploidy ($2n = 60$), and octoploidy ($2n = 80$) have been cited for subgenus *Ceresia* (Pers.) Rchb. of *Paspalum* (Saura, 1948; Tateoka, 1962; Gould & Soderstrom, 1967; Davidse & Pohl, 1972a, 1974, 1978; Pohl, 1980; Killeen, 1990; Hunziker et al., 1998). Species of this subgenus are distinguished by a winged rachis of the inflorescence, pilose spikelets, and a pale upper anthecium that is usually hyaline or membranous, with the tip of the palea not enclosed by its lemma. Two diploid counts were made for *P. buchtienii*, the first counts for this species; 10 bivalents were observed from microspore mother cells (Fig. 2A), and $2n = 20$ was observed from a mitotic metaphase of an anther wall cell. Also, the first count was made of *P. ceresia*, a tetraploid species with $2n = 40$ (Fig. 2B).

Paspalum blodgettii Chapm., *P. caespitosum* Flüggé, and *P. indecorum* Mez, species of group Caespitosa Chase, were diploid, agreeing with previously reported counts of $2n = 20$ (Davidse & Pohl, 1972a; Quarín, 1977; Quarín & Burson, 1991; Hunziker et al., 1998; Pagliarini et al., 2001), and tetraploid cytotypes, agreeing with previously reported counts of $2n = 40$ (Banks, 1964). Mexican *P. blodgettii* accessions are tetraploid with $2n = 40$, confirming a previous count by Banks (1964). Mexican *P. caespitosum* is a diploid with $2n = 20$, which agrees with determinations by Davidse and Pohl (1972a), and differs from the count reported by Banks (1964) that indicated a tetraploid cytotype with $2n = 40$. *Paspalum indecorum*, as previously reported by Quarín and Burson (1983) and Hunziker et al. (1998), is a diploid with $2n = 20$.

The group Racemosa Morrone, Zuloaga & Carbonó in *Paspalum* (Morrone et al., 1995) includes annual species of moist habitats up to 4600 m in elevation, all having the rachis flattened, deciduous, and foliaceous and the upper anthecium pale, cartilaginous, or crustaceous. Species are also anatomically characterized by having distinctive Kranz cells. Our count for the common species *P. candidum* (Humb. & Bonpl. ex Flüggé) Kunth is hexaploid with $2n = 60$ (Fig. 1H), and this agrees with several counts from Costa Rica and Honduras by Pohl and Davidse (1971) and Davidse and Pohl (1972a) but differs from previous diploid counts ($2n = 20$) (Davidse & Pohl, 1974) and tetraploid counts ($2n = 40$) (Hunziker et al., 1998). *Paspalum penicillatum* is a tetraploid with $2n = 40$, and some meiotic irregularities were observed in this species, with the presence of univalents (Fig. 1F). This is the first published count for this species. Finally, *P. prostratum* Scribn. & Merr. has $2n =$ ca. 40 (Fig. 2H), which agrees with previous studies by Davidse and Pohl (1974) and Reeder (1968). However, Pohl and Davidse (1971) also cited a hexaploid count for a Costa Rican specimen.

The Parviflora Chase group in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) consists mostly of small caespitose annuals with minute and pilose spikelets. *Paspalum clavuliferum* C. Wright was diploid, with $2n = 20$ and a regular meiosis. This count agrees with previous counts by Pohl and Davidse (1971), Davidse and Pohl, (1972a), and Reeder (1967).

The Virgata Chase group in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) includes tall species with a dark upper anthecium. Accessions of *P. commune* Lillo from Argentina have $2n = 40$, which confirms previous counts of this species as a tetraploid (Saura, 1941, 1948; Hunziker et al., 1998). Some meiotic anomalies resulting from an inversion heterozigosity were observed in this species, with the presence of univalents and bridges at anaphase II (Fig. 2C).

Two species were analyzed in the Livida Chase group (Chase, 1929; Zuloaga & Morrone, 2005), *Paspalum denticulatum* and *P. hartwegianum*. *Paspalum denticulatum* is a widespread American species with a high degree of variability in its vegetative and floral characters, which has led to the taxonomic establishment of several different entities now recognized under this species (Zuloaga & Morrone, 2005). *Paspalum denticulatum* was previously cited as a tetraploid with $2n = 40$ (Reeder, 1967; Gould, 1968; Davidse & Pohl, 1972b; Moraes Fernandes et al., 1974; Quarín, 1977; Quarín et al., 1982; Quarín & Burson, 1991; Hunziker et al., 1998) or a hexaploid with $2n = 60$ (Burson, 1975), but our Mexican collection was diploid ($n = 10$) (Fig. 1G). We found Mexican *P. hartwegianum* to have a count of $2n = 40$, whereas other reports had a hexaploid cytotype with $2n = 60$ (Gould, 1958; Davidse & Pohl, 1972b).

Paspalum ekmanianum, a member of the Lachnea Chase group (Chase, ined.; Zuloaga & Morrone, 2005), is an uncommon species characterized by its filiform blades and inflorescences with usually a single raceme and spikelets paired. It grows in Andean regions of southern Bolivia and northwestern Argentina, in open fields up to 2200 m in elevation. *Paspalum ekmanianum* has $2n = 20$ (Fig. 2F); this is the first reported count for this species.

The group Notata Chase of *Paspalum* (Chase, 1929; Zuloaga et al., 2004) includes caespitose perennials with inflorescences usually with two racemes and pilose or glabrous paired spikelets. The South American *P. ellipticum* was previously reported from Brazil as an octoploid (Moraes Fernandes et al., 1974), but our Brazilian collection was tetraploid, with $2n = 40$.

The group Fimbriata Chase in *Paspalum* (Chase, 1929) includes species with fimbriate spikelets, the upper glume having wings up to 3 mm long. One collection of *P. fimbriatum* was tetraploid ($2n$ = ca. 40), whereas other plants have been reported with $2n = 20$ (Banks, 1964; Gould & Soderstrom, 1967; Davidse & Pohl, 1974). Meiotic irregularities, such as the presence of 2 to 8 univalents, were observed in several cells. The meiotic behavior was normal but showed univalents in some cells, probably due to asynapsis or desynapsis at the end of diakinesis. Asynapsis occurs randomly in most individuals and is accompanied by a failure to form chiasmata, presumably caused by the interaction between the genotype and the environment.

The Decumbentes Chase group in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) is characterized by the presence of a first glume and axillary inflorescences and includes a total of 21 American species. Within it, the Argentinian species *P. glabrinode* is a diploid ($2n = 20$; Fig. 1D), the Mexican species *P. variabile* is a tetraploid ($2n = 40$; Fig. 2G), and the Bolivian species *P. inconstans* is a hexaploid ($2n$ = ca. 60). None of these species have been previously studied cytologically.

The highly polymorphic group Plicatula Chase in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) includes American species distributed from the United States to Argentina that are distinguished primarily by the presence of obovoid spikelets and a dark upper anthecium. Diploid accessions of *P. plicatulum* Michx. and *P. wrightii* Hitchc. & Chase, with $2n = 20$ (Fig. 2I), were analyzed. Brown (1950), Reeder (1967), Moraes Fernandes et al. (1974), Davidse and Pohl (1972b), Honfi et al. (1991), and Martínez and Quarín (1999, under *P. hydrophilum* Henrard) reported the same number, whereas Pozzobon et al. (2000) published counts for *P. plicatulum* of $2n = 40$. This species has a striking variation in its vegetative and floral characters, a fact that has led to the establishment of many entities now synonymized under this species (Zuloaga & Morrone, 2005). Several apomictic tetraploid cytotypes have been described for *P. plicatulum* (Quarín & Norrmann, 1987). *Paspalum glaucescens* Hack. is a tetraploid with $2n = 40$, a count that is in agreement with the previous counts recorded by Moraes Fernandes et al. (1974, under *P. yaguaronense*), Pozzobon et al. (2000), and Pritchard (1962, under *P. yaguaronense* Henrard). Quadrivalents, bivalents, and univalents were observed as meiotic configurations in this species (Fig. 2E). The morphological and cytological complexities of this group indicate a need for extensive and intensive study.

The group Paniculata Chase in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) includes a complex arrangement of 10 caespitose perennial species with flat blades, multiflowered inflorescences, and suborbicular spikelets. Diploid and tetraploid cytotypes have been published for the Paniculata group. The Bolivian material of *P. juergensii* Hack. was diploid

with $2n = 20$, confirming the previous counts by Moraes Fernandes et al. (1974), Burson and Quarín (1982), Dandin and Chennaveeraiah (1983), Pitman et al. (1987), and Pozzobon et al. (2000). Two accessions of *P. squamulatum* from Mexico were studied. One accession is a tetraploid with $2n = 40$, in agreement with a previous report by Pohl and Davidse (1971); the second is a diploid with $2n = 20$, which differs from previous reports for this species.

The group Dilatata Chase in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) includes four important forage species with multiflowered inflorescences and pilose spikelets that are ciliate along the margins. *Paspalum pauciciliatum* has $2n =$ ca. 38 chromosomes; the cells observed showed restitution nuclei (Rosemberg, 1927). Previous counts for *P. pauciciliatum* include a diploid cytotype with $2n = 20$ (Moraes Fernandes et al., 1974) and a tetraploid cytotype with $2n = 40$ (Honfi et al., 1991; Pozzobon et al., 2000).

Material of *Paspalum saccharoides* from Bolivia, belonging to group Saccharoidea Chase (Chase, ined.; Zuloaga & Morrone, 2005), is tetraploid with $2n = 40$, which differs from the count reported by Pohl and Davidse (1971) for a Costa Rican specimen ($2n = 20$). *Paspalum saccharoides* is an odd species within the genus *Paspalum*. The plants are tall and scrambling to 2 m, with long and plumose inflorescences, spikelets that are long-ellipsoid and densely pilose, the upper glume and lower lemma 2-nerved and hyaline, and upper anthecium hyaline and open at the summit. Pohl and Davidse (1971) indicated similarities between spikelets of *P. saccharoides* and those of the genus *Digitaria* Haller. Nevertheless, the genus *Digitaria* has a base chromosome number of $x = 9$.

The genus *Urochloa* has approximately 110 species present in tropical and subtropical regions of the New and Old World; several species have been extensively cultivated in tropical regions. Common basic chromosome numbers in the genus are $x = 7$, 8, and 9. *Urochloa fusca* (Sw.) B. F. Hansen & Wunderlin has $2n = 18$, a count that is in agreement with previously reported counts by Gould (1958, 1966, 1968), Gould and Soderstrom (1970), Pohl and Davidse (1971), and Reeder (1971) under *Panicum fasciculatum* with $2n = 18$. *Urochloa lorentziana* is a diploid with $2n = 36$ (Fig. 2D), but previous counts indicated an arrangement of $2n = 54$ (Morrone & Zuloaga, 1992).

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Cover illustration. *Capparis sicula* subsp. *mesopotamica* Inocencio, D. Rivera, Obón & Alcaraz, drawn by Jose-Antonio Barreña.